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Comparative Nesting Biology of the Bee Tribe Exomalopsini (Apoidea, Anthophoridae)

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CONTENTS

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ABSTRACT

New data on nesting behavior and ecology of the Exomalopsini are presented. The information is incorporated with previously published accounts to provide an overview of the nesting biology of this New World tribe throughout its geographic range. The account treats 23 species in seven genera. The specific subjects are: choice of nesting site, social organization, nest structure, provisioning, development, defecation, cocoon spinning, and cuckoo bee associations. A formal synoptic overview of the biological features of the tribe also is presented. The evolutionary relationships of the Exomalopsini with other anthophorine taxa are briefly discussed, as are relationships of the tribe with the cleptoparasitic subfamily Nomadinae.

INTRODUCTION

The present paper records new information on nesting behavior and ecology of bees of the anthophorine tribe Exomalopsini. Previously published data are synthesized with this information to present a comprehensive understanding of the biology of this group of bees, and to shed light on the evolutionary relationships of the taxa within the tribe and also of the tribe with other anthophorid taxa. Although the last objective can scarcely be realized because so few data are available, the great diversity within the Exomalopsini promises evidence for evolutionary interpretation.

The relationships of the Exomalopsini to the other taxa in the family are particularly interesting. Analysis of adult anatomy suggests that the tribe is the sister group of the other nonparasitic anthophorids (Michener, 1944; Michener and Moure, 1957). Because exomalopsines still retain some primitive features, they may be similar to the ancestor of the nonparasitic anthophorids. The evolutionary relationships of the parasitic anthophorids, especially the large subfamily Nomadinae, to the nonparasitic ones is not completely understood, but again, adult morphology indicates that the nomadines and exomalopsines may have shared a common ancestor. The possibility that the nomadines arose from a pollen-collecting exomalopsine-like ancestor leads to the question: what is there about exomalopsine behavior that might have led to the evolution of cleptoparasitism?

Exomalopsines are restricted to the New World, as are their close relatives, as defined by Michener and Moure (1957), except for the Old World tribe Ancylini, about which no biological information has been published. Classification for the Exomalopsini used here follows Michener and Moure (1957) and for the genus *Exomalopsis,* Timberlake (1980).

ACKNOWLEDGMENTS

I have been assisted in many ways in gathering data and preparing this manuscript. Finding and excavating nests is no easy task, and the following persons have worked with me to this end: Dr. Fred D. Bennett, Mrs. Marjorie Favreau, Ms. Ghisela Kreuger, Padre Jesus S. Moure, Mrs. Barbara L. Rozen, Mr. Kenneth C. Rozen, and Dr. F. C. Thompson.

Mr. John L. Neff allowed me to see his manuscript on the biology of *Eremapis parvula,* and Dr. Frank D. Parker showed me his manuscript on *Exomalopsis crenulata.* The information contained in those manuscripts has added to the completeness of the analysis section.

My fieldwork in Brazil and Trinidad, and some of my studies in southwestern United States were supported by grant nos. GB5407 and GB32193 from the National Science Foundation.

All the original observations on the genus

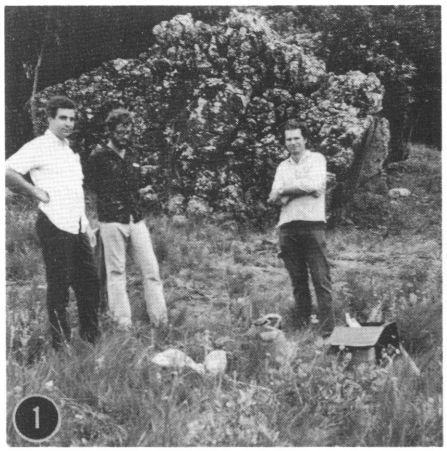


FIG. 1. *Tapinotaspis tucumana,* single nest, near equipment on the ground in the foreground, Vila Velha, Paraná, Brazil.

FIG. 2. *Monoeca lanei,* nests located in path in front of figure, near Rincão Tijucas do Sul, Paraná, Brazil.

Exomalopsis presented here were carried out at the Southwestern Research Station of the American Museum of Natural History over a period of 15 years. The long-term existence of the Station therefore has contributed substantially to the information in this paper and for that matter to many other papers by me and other persons interested in the Apoidea. I extend my thanks to Mr. Vincent D. Roth, Resident Director, for his hospitality and cooperation on many occasions.

I also extend my appreciation to the New York Zoological Society for the opportunity to stay at the William Beebe Memorial Laboratory on Trinidad in 1966 and 1968 where I investigated a nesting site of *Ancyloscelis apiformis.*

I thank my secretary, Ms. Deborah Hickman, for the careful preparation of this manuscript.

The following bee specialists have kindly reviewed this paper and offered valuable comments and suggestions: Mr. Robert W. Brooks, University of Kansas; Dr. George C. Eickwort, Cornell University; Dr. Charles D. Michener, University of Kansas; Mr. John L. Neff, Central Texas Melittological Institute; and Dr. Philip F. Torchio, United States Department of Agriculture. Mr. Roy R. Snelling, Natural History Museum, Los Angeles County, reviewed table 1.

SPECIFIC OBSERVATIONS

Paratetrapedia (*Trigonopedia*) *oligotricha* (Moure)

Michener and Lange (1958) provided limited data on this species that nested in a vertical bank (illustrated in Michener, 1974b, p. 40).

Paratetrapedia (*Paratetrapedia*) *gigantea* (Schrottky)

Oliveira (1962) in her description of the larvae of the species indicated that they had been recovered from the trunk of a rotting fallen tree.

Lanthanomelissa species

According to Oliveira (1966) this species nested horizontally in a vertical bank.

Tapinotaspis (*Tapinorhina*) *caerulea* (Friese)

Claude-Joseph (1926) gave considerable information about the nesting biology of the species under the name *Exomalopsis caerulea.* More recently Vogel (1974) presented additional data and determined that the stored provisions collected from flowers contained oil rather than nectar.

Tapinotaspis (*Tapinotaspoides*) *tucumana* (Vachal)[2]

DESCRIPTION OF NESTING AREA: Dr. F. Christian Thompson, Padre Jesus S. Moure, and I discovered and excavated five nests of this moderately large, nearly all black species in the vicinity of Vila Velha, a park in the state of Paraná, Brazil, between January 31 and February 5, 1974. One nest (fig. 1) was in the ground near the visitors center of the park, whereas all others were grouped several kilometers away; three of these were within 5 m of each other and the fourth was 100 m distant from the cluster of nests. Each nest was hidden in dense vegetation consisting mostly of grasses less than 1 m high; none was near trees or tall shrubs. Most entrances were not visible unless the surrounding plants were parted. These observations suggest that the species does not nest gregariously and prefers sites that are covered with abundant low vegetation.

In all cases the ground was horizontal to slightly sloping, moist, without stones or large pebbles, and easily excavated. Although numerous small roots penetrated the upper 15 to 20 cm of soil, no large roots were encountered.

NESTING ACTIVITY: Contrasting with many other Exomalopsini, each nest contained a single female. Three entrances (figs. 3–5) were on the ground surface and surrounded by tumuli of loose soil approximately 6 cm in diameter and 2 to 3 cm high. In one (fig. 5) the loose material, when blown away, left a hard core 1.7 cm in diameter surrounding the tunnel. Although this feature suggested a turret, it was not noted around other entrances and presumably was not a true turret such as that constructed by *Diadasia* but was caused by drying of moist soil. Two other entrances penetrated the fill of larger burrows (approximately 2 cm in diameter) which may have been scarab emergence burrows. One bee tunnel entered the side of the burrow about 3 cm below the surface; the other (fig. 4) penetrated vertically through the fill of the large burrow.

All main tunnels descended more or less vertically for their entire lengths, 23 to 33 cm (figs. 3–5). Each was circular in cross section, without a special lining, and open, except for one that had loose, coarse fill partway down (fig. 4). The tunnels tended to be about 5 mm in diameter, although one widened to about 7 mm at the cell level. Except for laterals leading to cells, tunnels did not branch.

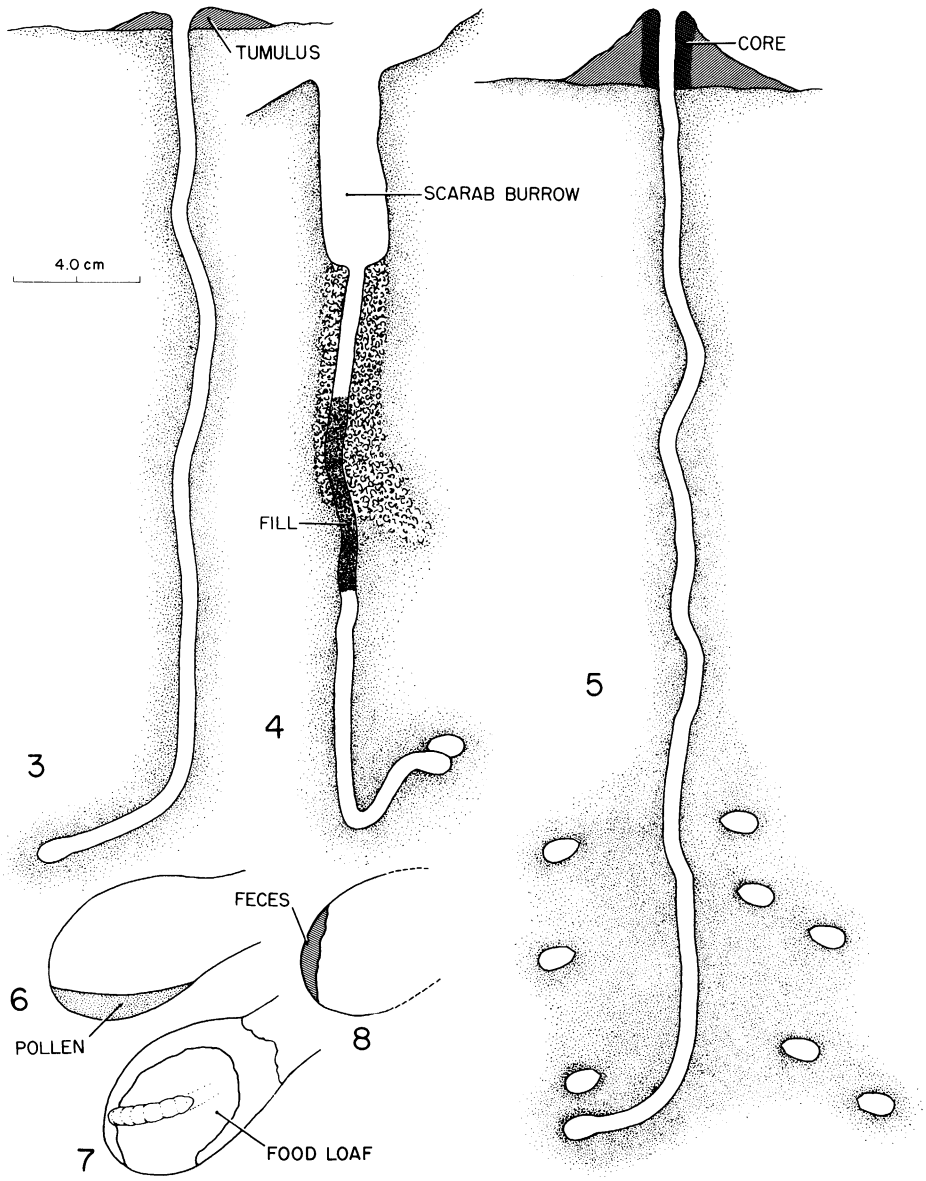
Laterals, all of which were filled after cell closure, ranged in length from 2 to 6 cm measured in a straight line from main tunnel to cell entrance. Approximately the same diameter as the main tunnel, they varied in direction, some curving gradually downward from the main tunnel, others leading horizontally, and still others rising to join the cells.

All cells were arranged singly (i.e., not in a linear series), had maximum diameters of 6.0 to 7.5 mm and maximum lengths of 10.0 to 10.5 mm (five measurements each), and were approximately 4.0 mm in diameter at the opening. They appeared to be slightly flatter on the bottom than on the top, and they sloped to the rear 20 to 35 degrees from the horizontal (figs. 6–8). No masoned (i.e., "built-in") wall of soil could be detected. The entire cell surface was smooth but uneven because of the coarse texture of the surrounding soil, and lined. In newly constructed cells, the lining was conspicuous and shiny and could be peeled with forceps. After construction this lining quickly became dull, perhaps as a result of a patina of fine black mold that grew sparsely over the surface. The lining was waterproof when tested with a water droplet. The lining darkened but did not melt at 700°F.

Cells were arranged randomly around the main tunnel. In general, older larvae were encountered nearer the surface, whereas younger individuals and eggs were found deeper in the ground, facts suggesting that the order of cell and lateral construction was from top to bottom. Although mature larvae and pupae were found lower than younger forms in one nest, we may actually have encountered cells from another nest.

The inside surface of the cell closure was a concave spiral of about three to four coils that were somewhat indistinct because of the coarse soil texture. Specimens of cells examined in the American Museum of Natural History revealed a closure that had no distinct outer surface, as did, for example, the

[2] Identified by Padre Jesus S. Moure.



FIGS. 3–8. *Tapinotaspis tucumana.* 3–5. Nests, side view. 6. Cell, side view, in the process of being provisioned. 7. Cell and food loaf, side view, showing young feeding larva. 8. Rear of cell, side view, showing position of feces. Scale refers to figures 3–5.

smooth, lined, concave outer surface of closures of *Exomalopsis.* Instead, the closure material seemed to grade into the fill of the lateral. All six closures preserved in the collection had short strands of fine brown fibrous material running between the soil particles in the plug. These twisted, flattened strands, somewhat like silk in appearance, also occurred in the fill of the adjoining lateral. The fibers may have been mold hyphae because one vacated cell (but not others) had similar strands extending from the cell wall into the cell lumen and even into the feces. However, strands did not occur in the soil surrounding either the cell or the lateral in any of the samples stored in the Museum. It

seems likely that the fibers were either hyphae or special material that the female bee deposited in the closure and lateral fill. The closure was waterproof on the inside when tested with a droplet, possibly because of the hydrofuge properties of the fibrous material. The fill in the lateral was also water repellent, in sharp contrast to the absorbent quality of the surrounding soil. The nature, source, and possible adaptive significance of the material deserves further investigation.

PROVISIONING: Although females in flight appeared to be transporting dry pollen to the cells, subsequent examination of pollen-laden females in the collection suggested that the pollen on the large, dense scopae was probably somewhat moist. The source of the pollen was not ascertained although pollen-bearing females were seen on a number of plant species. Early loads were placed evenly in a semimoist condition on the floor of the cell (fig. 6). After the total quantity had been brought in, the female shaped the food into an elongate loaf 7 mm long (three measurements) and 5 to 6 mm in diameter (two measurements) and attached it to the rear floor so that most of the loaf surface did not touch the cell wall (fig. 7). A number of loaves, bearing live eggs, had a highly convoluted, brainlike surface that possessed a stubble of whitish mold hyphae. In contrast, a number of food masses bearing young and intermediate larvae had a moist, yellow, fine, more even surface that lacked hyphae. Because it seems unlikely that early instars could consume enough surface material to remove all the hyphae and convolutions, the convoluted surface may have been an abnormality, perhaps an outbreak of a mold induced by certain weather conditions. Because all nests but one contained such provisions, the matter warrants further study.

DEVELOPMENT: One egg was found *in situ* in the midsaggital plane near the middle of the top of the pollen mass, its long axis paralleling that of the cell. Because oviposition behavior shows little variability in solitary bees, this placement will probably be characteristic of the species. Eggs were distinctly elongate, 3.0 to 3.15 mm long and 0.6 mm in diameter (two measurements each). Smooth, whitish, and somewhat shiny, they were slightly curved and perhaps slightly more rounded anteriorly than posteriorly. Young larvae fed as they slowly crawled over the soft, moist food surface (fig. 7), and, as they moved, made channels in the mass similar to those made by larvae of *Diadasia.* Mandibles were used to bite into the mass, as is also the case with *Diadasia olivacea* (Cresson) (Rozen, Eickwort, and Eickwort, 1978) and *Monoeca lanei.* Both large and intermediate-sized larvae pressed their dorsa against the cell wall as they crawled over the food, but how very young larvae moved is unknown. By the time larvae became intermediate in size, the pollen masses no longer adhered to the cell floors; the larva, curved around the mass, supported it entirely and prevented it from touching the cell wall at any point, as has been described for *Protepeolus singularis* (Linsley and Michener) (*ibid.*). Shortly after the larvae finished eating, they defecated. Feces were pressed to the upper rear of the cell (fig. 8) as elongate yellowish ribbons running parallel to the saggital plane of the cell. None of the excavated larvae became inactive after defecating but soon pupated. They spun no cocoons even though the labiomaxillary region, including palpi and the salivary lips, was fully developed as in cocoon-spinning larvae.

ADULT ACTIVITY: In contrast to that of most bees, the flight of this species (both sexes) was slow. Furthermore, individuals flew low over the vegetation and often encountered the taller stems and blades of grass, reducing their speed even more. The nests of this species would not have been discovered hidden in the dense vegetation had we not been able to follow the slow-moving, pollen-laden females with their black color and bright yellow pollen. We were further assisted in finding nests because returning females tended to fly directly to them rather than altering their course from one flower to another as do foraging females.

We saw no matings but collected numerous males flying through tops of the low vegetation in the same fashion as females. Both sexes were active during most of the day and a few females bearing pollen were still observed at 5:30 P.M. on one of the days.

Little can be stated concerning the seasonal cycle except that this species obviously has more than one generation a year as evi-

denced by larvae, after feeding, pupating in the laboratory.

PARASITISM: Immatures of no parasitic bee were recovered from the nest, but an apparently new species of cuckoo bee belonging to the nomadine genus *Parepeolus* (Michener, *in litt.*) was commonly seen flying in association with *Tapinotaspis tucumana* at a number of localities in Paraná. This mostly black parasitic form was difficult to distinguish in flight from *T. tucumana. Parepeolus* is believed to be a parasite of this species both because of coincidence of occurrence of the two and because a single adult female of the parasitic bee was recovered in one of the excavated nests of *T. tucumana.*

Monoeca lanei (Moure)[3]

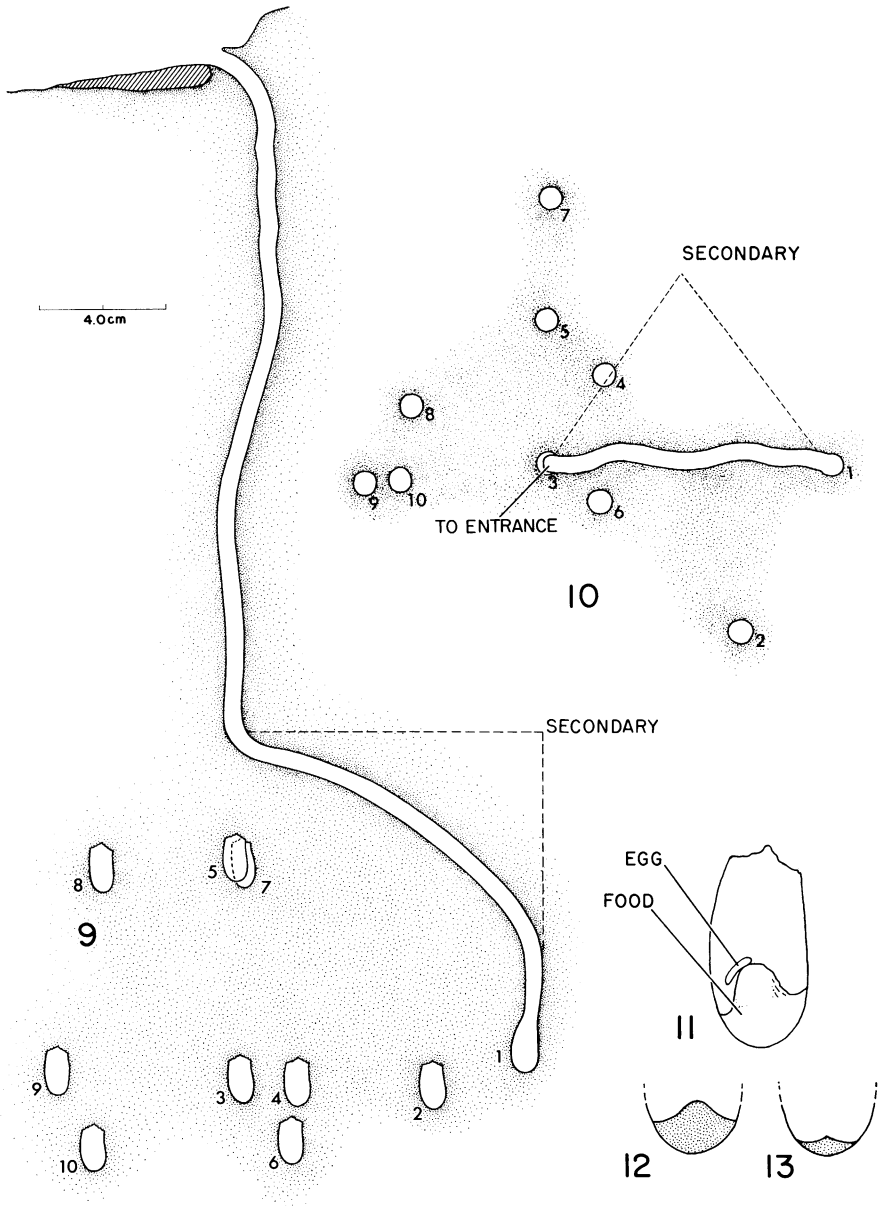
DESCRIPTION OF NESTING AREA: This species nested along a narrow dirt path (fig. 2) approximately 20 to 25 cm wide near Rincão Tijucas do Sul, Paraná, Brazil. Dr. F. Christian Thompson and I made the following observations on February 10, 1974. The path led across a level soccer field that was overgrown with tall grasses and other scattered plants. The path was 4 to 5 cm below the field surface in places, and during the course of our observations was intermittently trodden by people and farm animals. Trees and shrubs were sufficiently distant so as not to shade the site. Dry on the surface, the soil was moist immediately below and consisted of a fine claylike material, scattered coarser sandlike particles, and some organic debris but no stones, rocks, or large roots. The pollen plant was not discovered.

NESTING ACTIVITY: Six nests, each with a single female, were discovered along a stretch of 6 m, and several other nests may have been overlooked. All were at the edge of the path where the surface rose to meet the playing field. No cells from nests of previous generations were encountered. Several nest entrances were surrounded by distinct turrets (fig. 14) similar to those of some *Diadasia.* Turrets on other nests may have been destroyed by people or animals walking on them. The turrets were approximately 1.5 cm high and curved in some cases at nearly right angles. At least one was highly polished on the inside as was the main tunnel below. Tunnels turned downward immediately below the entrances and descended almost vertically. Circular in cross section and 5.5 mm in diameter, they were unusual in that the wall was shiny and coated with a waterproof material (tested with a droplet of water). Between the depths of 19 to 27 cm the vertical tunnel of each of the five nests excavated angled abruptly and then gradually curved downward until it reached an open cell. The lower curved section, here termed a secondary, had the same diameter as the main tunnel. In small nests a grouping of cells seemed to subtend a single secondary tunnel (fig. 15), as if all the cells had been constructed from the one secondary. However, in larger nests (fig. 10) the apparent random arrangement of cells suggested that each secondary branch led to a separate cell. If this is the case, the secondaries were actually "laterals" that were obviously filled with soil after cell closure. Secondaries were shiny on the inside like the main tunnel and presumably were also waterproofed. Secondaries narrowed only slightly at the cell opening.

Cells (fig. 11), arranged singly, were oriented vertically. Maximum cell length was 15 to 17 mm (three measurements) and maximum diameter, 7.0 to 7.5 mm (five measurements). To keep cells more or less intact during excavation was difficult, but one cell was obviously flatter on one side than the side opposite, and other cells suggested a similar asymmetry. This asymmetry as well as that of the provisions is similar to certain features in *Tapinotaspis tucumana.* Cells ranged in depth from 24 to 37 cm.

The cell wall showed no indication of being plastered with specially worked soil, and the cell lining was extremely thick, cracked easily so that it could not be peeled from the wall in spite of its thickness, and turned opaque whitish on drying. A piece of lining melted at slightly below the boiling point of water, contrasting sharply with the mere darkening of the cell lining of *Tapinotaspis tucumana* at 700°F. The lining dissolved slowly in ether but apparently not in xylene. The cell closure was a moderately concave spiral on the inside where it readily absorbed a water droplet when tested. The closure graded into the fill of the

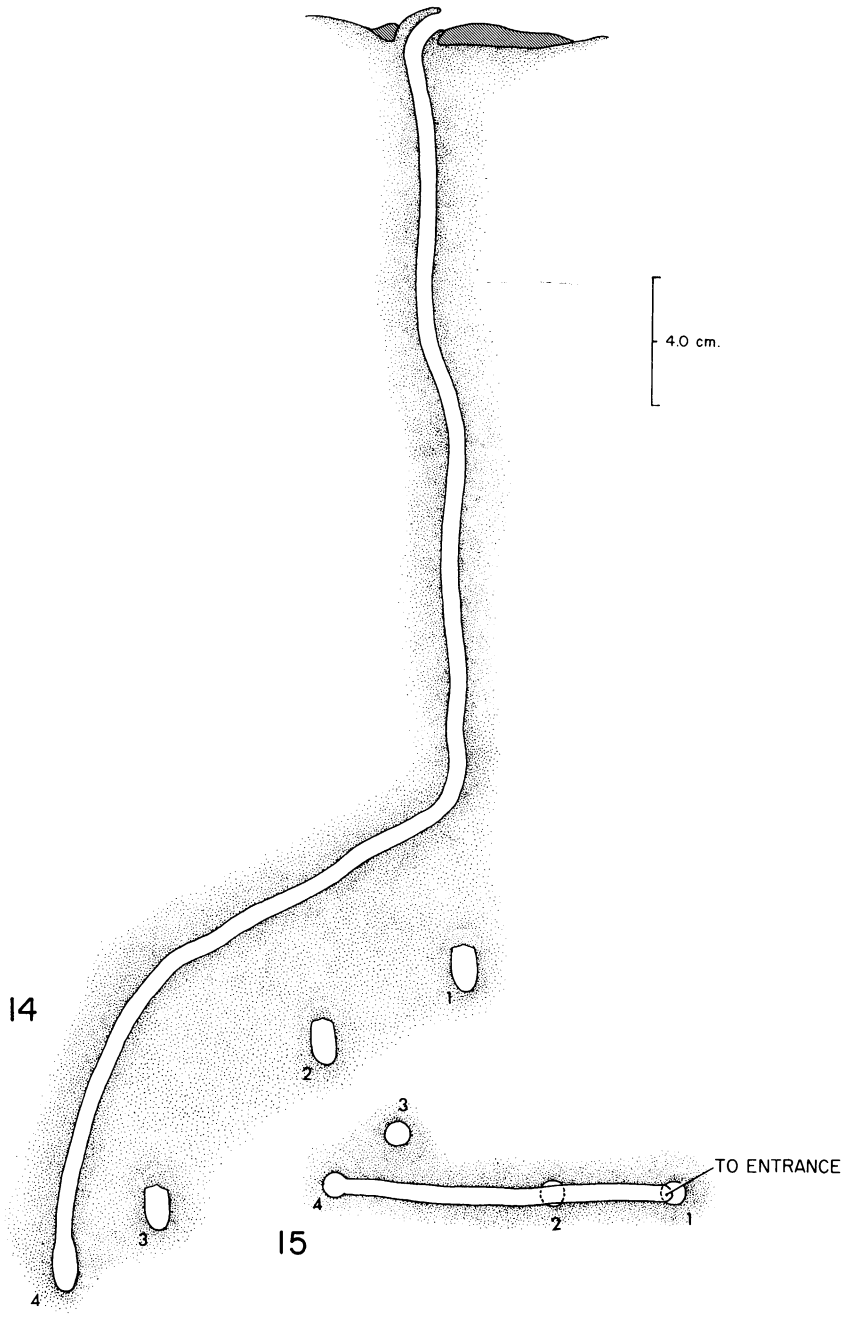
[3] Identified by Padre Jesus S. Moure.



FIGS. 9–13. *Monoeca lanei*. 9. Nest, side view. 10. Nest, same, top view. 11. Cell with egg and provisions, side view. 12. Bottom of cell with partly consumed provisions, side view. 13. Same, with provisions even more depleted. Scale refers to figures 9, 10.

secondary; there was no distinct, smooth outer surface to the closure.

PROVISIONING: Females transported provisions as a conspicuous, moist mass on their large scopae. During foraging, the female stored unworked loads of provisions in the bottom of the cell, a condition that parallels that of *Tapinotaspis tucumana* in spite of the difference in orientation of the cells. After transporting the final load, the female shaped the mixture into a tall, moderately dense loaf (fig. 11) in the center of the lower end of the cell. This loaf, without a foot, was "cemented" almost vertically by a somewhat more



FIGS. 14–15. Nest of *Moneoca lanei,* side and top views, respectively.

moist food mixture at the bottom of the cell. The surface of this cementing material tilted slightly upward toward the flat side of the cell in each case. The surface of the loaf was somewhat uneven, but no mold grew on it. The cementing mixture had a smoother surface than the loaf.

DEVELOPMENT: The slightly curved egg was deposited toward the top of the provision loaf and, at least in one case, was positioned to-

ward the curved side of the cell (fig. 11). The anterior part of the egg, pointing toward the cell closure, was more rounded than the posterior. In most cases the ends but not the middle of the egg were attached to the provisions, but, in one case (fig. 11), only the anterior part was attached. Because they were not glued to the food, eggs were easily dislodged accidentally when cells were opened. Somewhat elongate and white, with a smooth, shiny, transparent chorion, they measured 2.75 mm (two measurements) in length and 0.6 mm (one measurement) in maximum diameter. Upon hatching, the first instar remained *in situ* and apparently ingested liquid. Second instars crawled over the loaf as they fed. As the larva grew it consumed the provisions in such a way that the loaf became smaller but more acutely pointed at the top (figs. 12, 13). This species did not channel the provisions as do *Diadasia* and *Tapinotaspis tucumana.* At no time did the food mass separate from the bottom of the cell (figs. 12, 13). While curled more or less horizontally, last instars fed by ducking their heads to chew at the provisions on which they rested. Although a few cells contained considerable liquid, apparently most food masses did not normally acquire water but rather remained moderately firm while being consumed.

Our investigations were completed prior to defecation and possible cocoon spinning. Although the mouthparts of the larvae possessed such cocoon-spinning modifications as projecting salivary lips, these features may not always signify cocoon spinning on the part of the larva; see, for example, the discussion of *Tapinotaspis tucumana.*

ADULT ACTIVITY: Females were observed only over the nesting area as they returned with provisions. They approached moderately slowly, but after landing at the nest entrance, they entered without hesitation. In the larger nests, eggs as well as fully grown, predefecating larvae were encountered, suggesting that nesting had been taking place over a considerable period of time. However, since no pupae or postdefecating forms were found, this suggests that these bees do not nest and provision throughout the year.

PARASITISM: No cuckoo bees were associated with this site. Meloid larvae were found in two cells.

Monoeca schrottkyi (Friese)

Schrottky (1901) reported that this species, referred to as *Pachycentris schrottkyi,* nested in a bank, but he gave no further information.

Monoeca species

Michener and Lange (1958) briefly referred to a nest of an unidentified species in this genus.

Exomalopsis (*Exomalopsis*) *aureopilosa* Spinola

Zucchi (1973) carefully examined nests of this species and recorded his findings in his doctoral thesis. From the description and his well-prepared drawings, it is clear that he misinterpreted Rozen and MacNeill's (1957) description of the "foot" on the food loaf. What he recorded as the foot seems to be a special structure at the bottom of the food mass which is in a vertical cell.

Exomalopsis (*Exomalopsis*) *globosa* (Fabricius)

Considerable explicit ecological and life history information on this species and the one following was recorded by Raw (1977). In addition to details about nests, he included information on predation, mortality, fecundity, and cooperation among adult females in nest building.

Exomalopsis (*Exomalopsis*) *similis* Cresson

The biology of the species was treated and compared with the one above by Raw (1977).

Exomalopsis (*Megomalopsis*) *fulvofasciata* Smith

Zucchi (1973) reported that two nests of this species were found on a narrow path with a number of nests of *E. aureopilosa.*

Exomalopsis (*Phanomalopsis*) *solani* Cockerell

Although both Michener (1966) and Hurd and Linsley (1975) have noted that a number of females occupy the same nest, nothing else has been recorded about the nesting biology

of this common species from the southwestern part of the United States, except that *Paranomada velutina* Linsley is a cleptoparasite in its nest (Rozen, 1977b). The following information is derived primarily from cells preserved in the American Museum of Natural History, and from photographs of the cells and provisions taken in 1967.

DESCRIPTION OF NESTING AREA: Two nests of the species were excavated at 1 mile north of Rodeo, Hidalgo County, New Mexico. One nest, excavated on August 28, 30, and 31, 1967, by Ghisela Kreuger and myself, yielded the *Paranomada velutina* larva described by Rozen (1977b), and the other nest, excavated on August 15, 1974, by Kenneth C. Rozen, was occupied by at least 12 females. The ground surface was probably horizontal or nearly so in both cases. Cells from the 1967 nest were in soil of coarse granular particles intermixed with a fine reddish claylike material. The soil from the 1974 nest was fine and even-grained.

NESTING ACTIVITY: Cells collected in 1967 ranged in length from 8.0 to 9.1 mm (six measurements) and 5.2 to 5.6 mm in maximum diameter (eight measurements). Two cells from the 1974 nest were 5.2 and 5.5 mm in maximum diameter. No apparent difference could be detected between the cell wall in cross section and the surrounding soil in the 1967 nest, so that the cell wall apparently had not been plastered. Similarly, no masoned cell wall could be detected in the 1974 nest, but samples in the collection suggest that the cell wall may have been somewhat harder than the surrounding soil. In cells from both nests, the lining was partly shiny, waterproof when tested with a droplet, and smooth, except where large soil particles protruded. No visible change could be detected in the color or nature of the lining when heated on a hot plate to 700°F. Cell orientation was not recorded, but cells were slightly flatter on one side than the other, and the angle of the plane of the closure did not form a right angle with the "longitudinal axis" (as defined under *E. solidaginis*) of the cell, as was also the case with *E. compactula* (fig. 16) and *solidaginis* (figs. 17–24). Consequently, the flatter side of the cell was shorter than the opposite side.

The cell closure on two cells was 4.0 mm in diameter and in all cells was a concave spiral with four to five coils to the radius on the inside and smooth and deeply concave on the outside. Two of the closures were 2 mm thick at the periphery and about 1 mm thick in the middle. The outside, like the cell wall, was waterproof when tested with a droplet of water, but the inside surface readily absorbed water. Laterals were filled with soil.

PROVISIONING: Several photographs of the food loaf taken in 1967 show that it was similar in general shape to those of *E. chionura, solidaginis,* and *consobrina,* with a flattened top surface[4] on which the egg was positioned, and a somewhat truncated front end as viewed from above. As viewed from the side, the front end sloped downward and backward as if drawn into a ventral foot, which may or may not have been present. The surface of the loaf was smooth and moist, and the rounded rear of the mass fitted evenly against the rear of the cell. Dimensions (single measurements) were loaf length, 5.0 mm; height, 3.3 mm; and maximum width, 3.2 mm.

DEVELOPMENT: Two eggs were in the midsaggital plane on top of the food masses. At least one had its anterior end closest to the cell closure, and slightly less than 1.0 mm from the front end of the loaf. Its position, therefore, was essentially as shown for the early instar larvae of *E. solidaginis* (fig. 20). It was white and curved. No cocoons were collected from either nest, and the salivary lips on mature larvae were only slightly produced. Consequently, no cocoons are apparently spun by this species. Several cells in the collection had linear sequences of nearly spherical fecal pellets over most, if not all, of the cell wall. Although the quantity of feces in these cases suggested that larvae had only begun to void, the pattern suggests that feces are applied to the entire cell wall. No information is available on whether or not feces are applied to the inner surface of the cell closure.

PARASITISM: Rozen (1977b) described the mature larva and pupa of *Paranomada velutina* collected from the 1967 nest. The rate of parasitism by this cuckoo bee was high; at least 50 percent of the cells contained *Paranomada* eggs or larvae.

[4] Description of food loaf and egg here assumes that the cell is essentially horizontal.

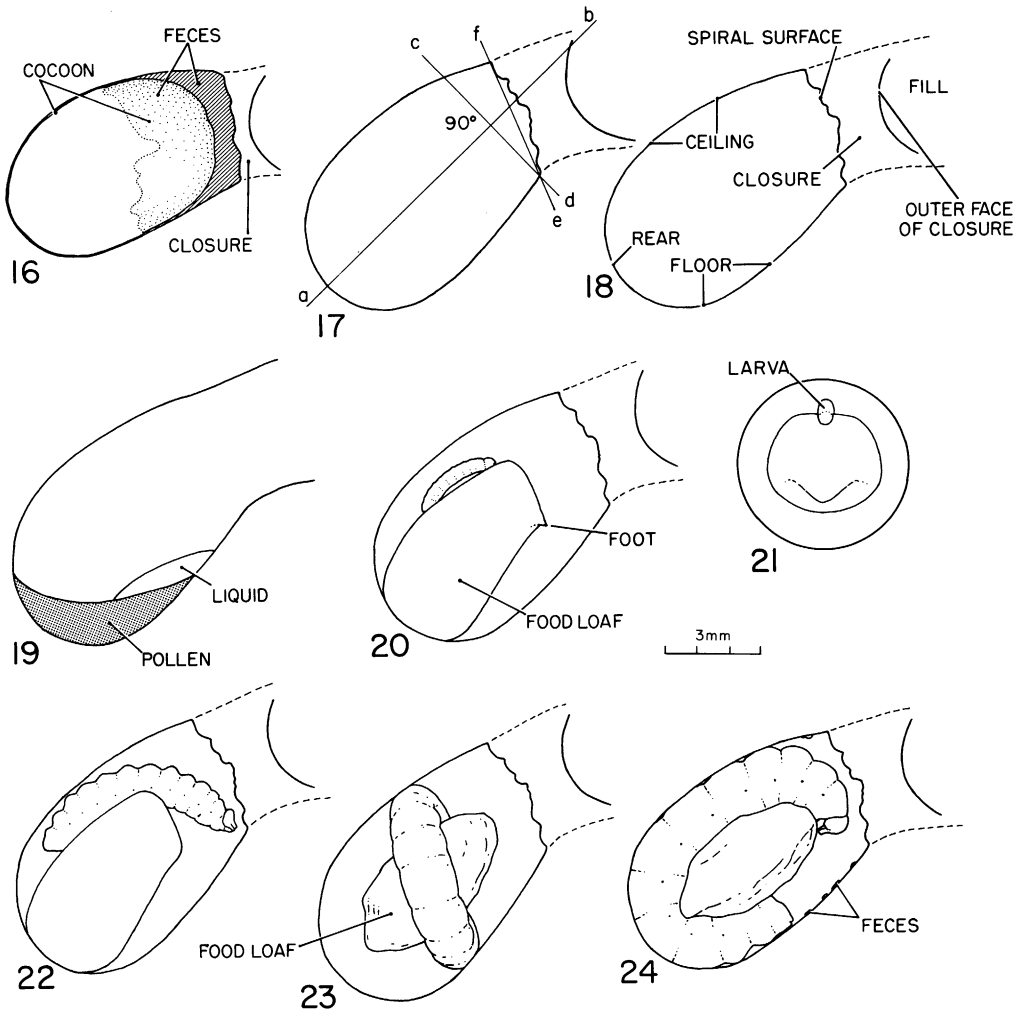


FIG. 16. *Exomalopsis compactula* cell containing feces and cocoon, side view.

FIGS. 17–24. *Exomalopsis solidaginis.* 17. Cell, side view, showing method of taking measurements. For further explanation, see text. 18. Same, showing terminology used in text. 19. Same, being provisioned. 20. Same, showing fully formed provisions with early instar. 21. Same, front view, showing position of provisions and early instar. 22. Same, side view, with third instar. 23. Same, showing fourth instar circling grooved food loaf. 24. Same, early fifth instar starting to defecate while feeding on grooved food loaf. Scale refers to all figures.

Exomalopsis (Phanomalopsis) solidaginis Cockerell[5]

DESCRIPTION OF NESTING AREA: I discovered a single nest of this species in the center of a nearly horizontal, infrequently used, dirt roadway 20 miles south of Animas, Hidalgo County, New Mexico, on September 8, 1977, and excavated it on September 14, 1977. Twelve females were collected either entering, exiting, or in close association with the nest; and 14 others, possibly representing re-

[5] Identified by J. G. Rozen, Jr., but the identification is not certain. Extensive series of adult *E. solani* and a shorter series of *E. solidaginis,* both identified by P. H. Timberlake, in the collection of the American Museum of Natural History, lead me to suspect their distinctiveness and therefore their validity as separate species. Females taken from the nest display more of the characteristics of *solidaginis* as identified by Timberlake (1980)

turning foraging females, were collected while flying as if lost over the roadway after I started excavations. The entrance as well as the surrounding ground was unshaded by the ground cover of low herbaceous vegetation and was not in danger of being flooded in the event of heavy rains. The compact, claylike soil was hard and dry on the surface but moist and more easily excavated below 10 cm. It contained few stones or roots.

Two more nests were found within 1 m of each other at 13 miles southwest of Apache, Cochise County, Arizona, on August 30, 1983 (fig. 25). The larger nest was partly excavated the next day, and 35 females and 1 male were recovered from it. The smaller one contained 17 females and 1 male. Like the Animas site, the area was nearly level, unshaded, and supported low sparse vegetation such as *Lepidium, Mentzelia,* and *Euphorbia.* The soil was dry on the surface and had few roots and pebbles, but at about 25 cm depth it contained many rocks and pebbles.

NESTING ACTIVITY: The nest entrances, without tumuli or turrets, were circular in cross section, and slightly beveled. The Animas nest was excavated more completely than the Apache one. The main tunnel of the Animas nest, 4.5 mm in diameter, descended vertically with only slight meandering to a depth of 42 cm. The tunnel possessed no chambers or branches in the upper reaches, but between depths of 42 and 58 cm it branched a number of times at irregular intervals, with resulting tunnels radiating outward in all directions in a meandering fashion. At this general level 130 cells, containing all stages of larvae and eggs as well as meloids, were excavated as were cells from previous generations. The cells extended over a horizontal area of about 58 by 40 cm and the nest was probably even more extensive. The tunnels seemed unlined and most were open, except that those tunnels (laterals) leading to cells were plugged with soil. Some tunnels other than laterals may also have been filled, as a number of cells seemed considerably removed from open tunnels.

The Apache nest was essentially similar except that its main tunnel descended only to about 25 cm in depth. At this point it branched numerous times with subsequent tunnels leading nearly horizontally. Apparently the hard, pebble- and stone-filled lower soil prevented the females from descending farther, with the result that numerous freshly provisioned and vacated cells were found between the depths of 25 and 35 cm.

Cells at the Animas site (figs. 17–24), arranged singly, were oriented somewhat less than 45 degrees from horizontal, usually near main tunnels, and had the closure end higher than the rear. They ranged from 7.5 to 8.5 mm long and 5.0 to 5.5 mm in maximum diameter (eight measurements). The inner surface was extremely fine grained, smooth, and moderately shiny throughout, and the earthen cell wall was thick and usually somewhat harder than the surrounding soil. As a consequence, cells often could be identified and extracted from the ground without being opened. The hardened wall was thickest (approximately 1.0 mm) at the rear of the cell, whereas elsewhere, especially the floor, it was often noticeably thinner (approximately 0.3 to 0.5 mm). Except for hardness, there was no indication that the wall had been fabricated by the female. Although the hardness may have been caused by the female mixing soil with some secretion, it could also have resulted from a secretion applied to and absorbed by the inner surface of the cell.

Cells at the Apache site agreed with those from Animas except that the walls were not noticeably harder than the surrounding soil. However, there was a strong suggestion that not only the cell walls but also the burrow wall might have been masoned. For example, parts of dead *Exomalopsis* individuals were buried in the walls. Cell orientation at the Apache site may have been more variable (perhaps because of the pebbly substrate), with cells seeming to range from 35 degrees to 80 degrees from horizontal.

Because of the numerous cells recovered from the Animas nest and the hard consistency of their walls, a detailed investigation of cell symmetry was possible. Several cells were opened and trimmed so that their shape could be carefully drawn with the camera lucida and analyzed in longitudinal cross section. As can be seen in figure 17, the major

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than those of *solani,* and therefore I provisionally use the former name. Cells of this species were also smaller than those of *E. solani,* corresponding to a recorded size difference between the two.

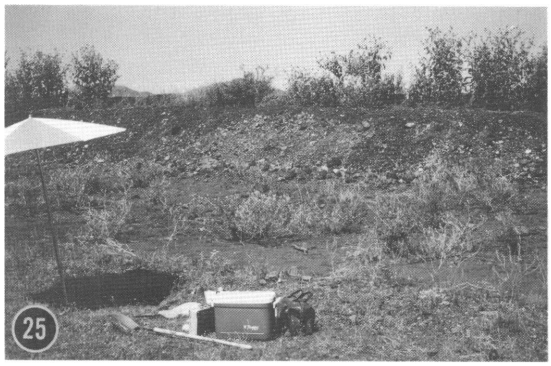


FIG. 25. *Exomalopsis solidaginis,* nesting area 13 miles southwest of Apache, Arizona. Two nests were found at edge of barren area just behind the ice chest.

FIG. 26. *Exomalopsis sidae,* nesting area 5 miles north of Willcox, Arizona. Nests were scattered from umbrella next to car to net in middle foreground.

part of the cell was divided into an upper and lower half by drawing line *ab* from the rear point of the cell so that areas above and below the line and behind a perpendicular (*cd*) to it were approximately equal. This line only approximated the "longitudinal axis" of the cell because of the asymmetry of the upper and lower halves and because the plane of the periphery of the cell closure (line *ef*) was not at right angles to this line. From figure 17 it appears that the rear (lower) part of the cell was nearly, but not quite, symmetrical, the floor being slightly flatter than the ceiling. Unquestionably, the ceiling was longer than the floor, because the plane of the cell closure (*ef*) was not perpendicular to *ab*. This cell and closure configuration was characteristic of all cells in the nest. The extremely thin, transparent lining did not melt when heated to 700°F. on a hot plate, nor did it change in color or texture in any other way.

The cell closure at both sites was a shallow, concave spiral on the inside with four distinct, and well-defined rows to the radius. The inner surface of the cell closure was not waterproof when tested. The outside of the cell closure was smooth and more concave than the inner side. The outer surface was darkish and waterproof, not unlike the inner surface of the cell itself. Animas closures were approximately 1.5 to 2.0 mm thick in the middle, and 3.0 mm at the edge, and their diameter was approximately 4.0 mm. A single Apache closure was 1.5 mm thick at the edge, and three measured 3.2 to 3.4 mm in diameter.

PROVISIONING: Two cells were encountered as they were being provisioned. The moist pollen load was appressed to the rear of the cell and the cell floor. One cell (fig. 19) had a drop of liquid (presumably nectar because it was miscible with water) extending from the pollen surface onto the cell floor. Newly formed provisions were shaped as in figure 20, and in each case the rather wide, rounded rear end was attached to the rear of the cell by a droplet of liquid. The foot, which in some other species of *Exomalopsis* (e.g., *chionura,* Rozen and MacNeill, 1957, figs. 1–4; *consobrina,* Rozen, 1977b, fig. 1) touched the cell floor, was smaller than in the other species, and did not reach the floor. The general shape and position of the food mass (fig. 20) were constant in the numerous cells examined, although the size varied. The orange-yellow, moist loaf, somewhat flattened on top, was 5.0 to 6.1 mm in length (nine measurements), 3.2 to 4.0 mm in width (nine measurements), and 2.9 to 3.5 mm high (eight measurements), and had a smooth surface. Cells with provisions gave off a fermented, cheesy odor when first opened.

DEVELOPMENT: Curved, translucent white, shiny eggs were deposited on the anterior top of the food masses in the midline of the cells with only the front and rear ends touching the surface.

The following comparative anatomical

study of larvae from the Animas nest revealed five larval instars, a figure corresponding to Oliveira's (1966) documentation in the case of *Lanthanomelissa.* Nonetheless, Rozen, Eickwort, and Eickwort (1978) observed only four instars in *Diadasia olivacea,* so that the number of larval stadia deserves further careful attention. The anatomical study was based on a total of 94 larvae preserved from the nest, including six postdefecating, quiescent, mature larvae; 56 actively feeding and/or defecating fifth instars; 17 fourth instars; nine third instars; four second instars; and two first instars. Because the structures of the second instar were visible through the nearly transparent cuticle of the first instar, the first instar was difficult to distinguish from the next instar. Nonetheless, the cuticle of the head and anterior part of the body of the first stage larva displayed distinct mouthparts (including a short unpigmented but apically pointed mandible), as well as spiracles and tracheae. As indicated above, the first instar apparently remains in the same position as the egg, and there was no pollen in the dissected intestinal tract of either specimen. Perhaps first instars consume only liquid from the food mass, as has been suggested for *Diadasia olivacea* (*ibid.*).

Second instars bore mandibles, each of which was slightly pigmented at the tip and possessed a small, pointed subapical ventral tooth. Maxillary palpi were distinct, but small and nipple-like, and not as high as their basal diameter. Because the abdominal venter IX was slightly protuberant, this instar may have been able to crawl, but I made no direct observations of this. The intestinal tract of one about to molt was packed with abundant pollen, proving that this instar ingests more than liquid. Increase in body girth and length also attested to its eating.

The mandibles of the third instars were distinctly pigmented at the entire apical end, including the ventral tooth. The maxillary palpi projected and were about as long as their basal diameter. One larva was found on the top front of the pollen mass, as illustrated in figure 22. This instar is believed to be ambulatory in that the abdominal venter IX projected strongly and small median ventral tubercules (probably eversible in nature) occurred on the midline between most of the body segments. These tubercules, though small, were quite visible on most specimens in which the integument was somewhat distended.

The mandibles of the fourth instar were even more darkly pigmented than those of the third, with the ventral subapical tooth now more apical in position. The maxillary palpi were longer than their basal diameter. This instar was able not only to crawl while feeding over the now oblong, ridged food mass, but also to detach the mass from the rear of the cell (fig. 23) and support it in the center of the cell with its body. The food surface, by this time, had become much more moist, so that distinct feeding channels remained in the soft surface as the larva crawled. Fourth instars were found in various positions in the cell. None was seen to defecate.

The fifth and last larval instar (fig. 24) consumed most of the provisions. The mandibles were thinner subapically in relation to their overall size than those of other instars, and maxillary palpi were longer than their basal diameter. The larvae continued to move in relation both to the wall and to the food mass. The loaf diminished in size with the larval feeding while the larva cradled it so that it did not touch the cell wall or the feces. Larvae fed rapidly; one took 36 bites during a 10-second period, or about four bites per second. During the beginning of this stadium larvae started defecating, applying yellow feces as rows of small ovoid smears on the cell wall and closure. After provisions were consumed, the feces appeared as somewhat flattened pellets appressed more or less evenly over the entire surface of the cell, although the cell closure may not have been so densely covered as the wall. No cocoon was spun, as revealed both by six postdefecating larvae lacking them and by the recessed labiomaxillary region of the larval heads. The dark color of the feces in cells of postdefecating larvae suggested they may have been overwintering from the previous year. No pupae occurred in the nest at the time of excavation.

The Animas site produced a wide range of instars on September 14, as discussed above, whereas the Apache site yielded only eggs and very early instars on August 31. Although the sample size was small at Apache, the differences between the two may have been real,

a result of the different dates of collection.

ADULT ACTIVITY: Females were seen entering and leaving the nest from 10:00 A.M. to 3:30 P.M. Although some females were found in the Animas nest, they were few in number (four or five) and no adult males were observed either in, or in the vicinity of, the nest. However, the partly excavated nest at the Apache site yielded nine females, and a male emerged from each of the two nests there.

PARASITISM: No cuckoo bees, either as adults or as immatures, were found in the Animas nest. Of the 130 cells uncovered, 10 were inhabited by large, active meloid larvae. At the Apache site, four females of the cuckoo bee *Paranomada nitida* were collected while examining the entrance of the larger nest, one while flying around the entrance of the smaller nest, and still another as it emerged from the smaller nest. The excavated nest produced three first instars and one second instar of the cuckoo bee. Several of these larvae were associated with flaccid *Exomalopsis* eggs which they had undoubtedly killed with their strongly curved mandibles. Two first instars measured 1.5 mm long, the second instar 1.8 mm. The head capsule of the first but not second instar was darkly pigmented. A single oviposition insertion in the cell wall consisted of a hinged, irregular flap, 0.5 mm long and 0.3 mm wide, similar to the one described for *Paranomada velutina* (Rozen 1977b).

Exomalopsis (*Anthophorula*) *compactula* Cockerell[6]

Two nests of this species were excavated by me and Barbara L. Rozen on August 30, 1966, and September 2, 1966, at 5 miles north of Rodeo, Hidalgo County, New Mexico. Its immature stages as well as those of its parasite, *Triopasites penniger* (Cockerell), were recovered (Rozen, 1977b). Brief notes on nest structure were taken, and samples of nest components were preserved in the American Museum of Natural History.

NESTING ACTIVITY: Both nests were situated in nearly horizontal ground. Each entrance was open, somewhat irregular in shape, not near an obvious marker such as a stone or twig, and without a tumulus. One nest was occupied by at least two females, and both old and current cells were present in the nests. The main burrow, circular in cross section, was 4.0 mm in diameter. Its wall seemed to be lined with finer material than the substrate, and was not waterproof when tested with a droplet of water. Each main burrow descended vertically in an irregular fashion for 20 to 25 cm and then branched, and at least one then branched numerous times. Some sections seemed filled with soil, whereas others were open. Laterals were filled with soil that was less consolidated than the cell closure.

There seemed to be no pattern to the distribution of occupied cells in relation to vacated cells within the nest. Most cells seemed to be tipped 10 to 30 degrees from the horizontal with the closure end higher than the rear. Cell arrangement needs further study but in one case, two in linear series were 4.0 mm apart. Others may have been arranged singly, and most seemed clumped side by side in close proximity. Cells in the collection ranged from 6.2 to 7.2 mm in length (three measurements) and from 4.2 to 4.5 mm in maximum diameter (six measurements), and two were 3.5 mm in diameter at their connections to the laterals. Cell walls were harder than the surrounding soil, and may have been plastered with specially prepared material because their texture seemed to be finer than that of the substrate. Cell shape seemed identical with that of *E. solidaginis,* that is, somewhat flatter on the bottom, and, at least in some cells, with the plane of the closure not at right angles to the "longitudinal axis" of the cell. The internal surface of the cell was extremely smooth and polished, and was waterproof when tested with a droplet of water. One but not the other of two cells that had not yet been provided with a closure was lined with a nearly transparent material over the rear wall in addition to the normal polished lining. When tested by being placed on a hot plate, this lining shriveled but did not puddle, vaporize, or darken at 700°F. Fragments of this and other cell walls, when placed on a hot plate, did not change in appearance, even at 700°F.

[6] Identified by P. H. Timberlake.

The cell closure on the inside was a nearly flat spiral of approximately four coils, in some cases slightly convex and in others, slightly concave. On the external surface, the closures were strongly concave and smooth. Both surfaces were waterproof when tested with droplets. The closures were 3.4 to 3.5 mm in diameter on the inside (three measurements), approximately 1.0 mm thick at the periphery and 0.5 mm thick in the middle.

PROVISIONING: No information available.

DEVELOPMENT: In several cells (fig. 16), there was clear evidence that most, if not all, of the feces were applied to the cell closure and very front of the cell, so as to obscure the cell closure from the inside. In old cells from which adults had emerged, there was an indication of a band of feces around the cell opening, and the cell contents consisted of mixed soil (presumably closure material) and feces. These observations suggest that the feces are normally plastered at the front end of the cell. In several other cells, feces seemed to have been distributed elsewhere, but those cells may have been inhabited by larvae of *Triopasites*. No cocoons were detected in the field, but each of two cells preserved in the collection had an extremely thin cocoon of almost transparent parchment-like material appressed to the cell wall and inner surface of the feces, with the result that the larva was walled-off from the fecal mass. The presence of cocoons and the placement of feces deserve confirmation and further study.

PARASITISM: *Triopasites penniger* was discovered to be a cuckoo bee in the nests of this species (Rozen, 1977b). Early stages of a mutillid were also recovered.

Exomalopsis (*Anthophorula*) *crenulata* Timberlake

Parker (in press) provided some valuable information on the nesting habits of this species.

Exomalopsis (*Anthophorula*) *torticornis* Cockerell

Hicks (1936) reported that four females were associated with a single nest of this species.

Exomalopsis (*Anthophorisca*) *chionura* Cockerell

Rozen and MacNeill (1957) described nesting and other aspects of the life history of this species. Specimens of cocoons and nests in the California Insect Survey, referred to in that paper, on re-examination yielded the following new observations: Water absorption was difficult to test because the soil preserved in the laboratory appeared very dense and absorbed a water droplet slowly. Nonetheless, a droplet placed on the burrow wall was absorbed rather quickly in the two cases tested, indicating that there was no special burrow lining. Several cell walls similarly tested seemed to absorb water at a slower rate than the soil, suggesting a waterproof lining. The nearly flat, spiral inside surface of two cell closures absorbed water moderately quickly, an indication of a lack of waterproofing. The strongly concave outside surface bore the distinct impressions of the female's pygidial plate and absorbed water droplets rather slowly so that it may have been at least partly waterproof. Cell linings did not melt at 700°F. Laterals leading to cells were filled with soil. Although samples were insufficient to determine whether cells were slightly flattened on the bottom, a number of closures were not at right angles to the "longitudinal axis" of the cells. All preserved cocoons were rounded at the front end and none conformed closely to the shape of the closure and cell rim. The front ends of several cocoons *in situ* were so rounded that some space existed between the cocoon and the front of the cell. Only the most frontal point of the cocoon touched or nearly touched the center of the closure.

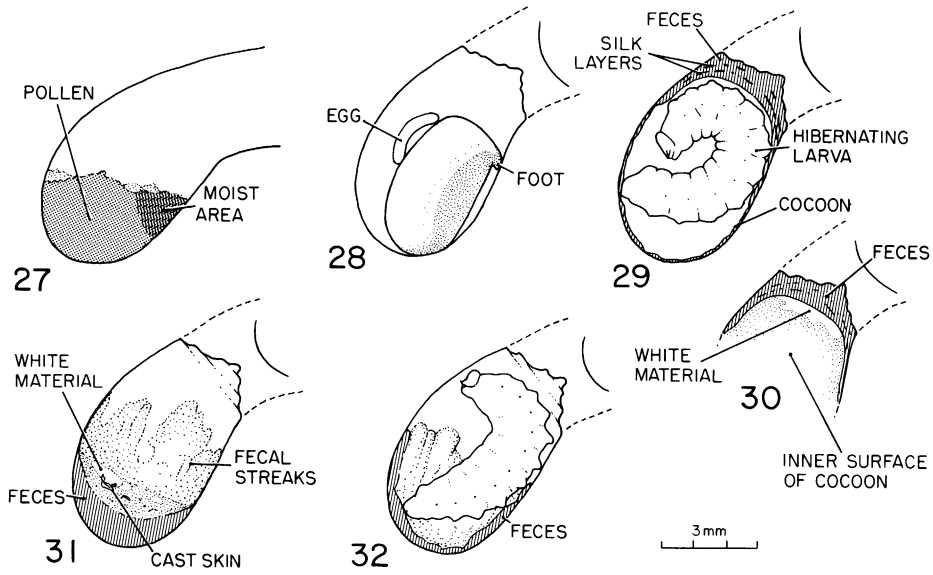
Exomalopsis (*Anthophorisca*) *consobrina* Timberlake

The nesting biology of this species, called *E.* near *chlorina,* was briefly treated by Rozen (1977b).

Exomalopsis (*Anthophorisca*) *sidae* Cockerell[7]

Barbara Rozen and I discovered numerous adults of this species foraging and mating on

[7] Identified by J. G. Rozen, Jr.



FIGS. 27–32. *Exomalopsis sidae,* cells, side view. 27. Open cell containing preliminary loads of fluffy pollen. 28. Egg and shaped food loaf. 29. Overwintering larva in cocoon. 30. Front end of cocoon, showing position of white fecal material. 31. Cell from which pupa had been removed, showing lack of cocoon and position of fecal material. 32. Cell containing hibernating larva of *Melanomada sidaefloris* and its feces.

the flowers of *Sida,* 5 miles north of Willcox, Arizona, on August 21, 1983. Returning on August 29, I found and marked four nests. Another two were found when Marjorie Favreau and I revisited the site on Sept. 3, 1983. A total of three nests were excavated.

DESCRIPTION OF NESTING AREA: As in the nest of the same species reported by Rozen (1977b), all six entrances were on the gently sloping shoulder of a road between 2.5 and 3 m from the edge of the pavement, among the grasses and abundant *Sida* that grew there. The plants were mowed periodically as part of highway maintenance. Undoubtedly other nests occurred along the shoulder, considering the large number of adults on the flowers; the six nests were scattered along 8 m. None of the entrances were shaded extensively by the low, scattered vegetation. The soil was fine grained, almost claylike, with few stones and roots. Dry on the surface, it was visibly moist below 5 to 7 cm and cracked in many places because of the drying of the upper 10 cm.

NESTING ACTIVITY: Nests were generally occupied by more than one female: two nests had at least eight; one nest had four; two had two; and one had one. Males were not seen leaving any of the nests.

The entrance of each of the six nests was open, not near a ground marker, and without a tumulus. Entrances ranged in diameter from 2.75 to 3.0 mm. The open main tunnel, 3.5 mm in diameter, descended almost vertically to the level of the cells. Although one burrow branched 8 cm down, branching generally began approximately 20 cm in depth, with branches dividing, redividing and descending at various angles. In three nests almost all cells were encountered between 20 and 30 cm in depth.

The main tunnel and branches were unlined, not waterproof, and often, if not usually, bore clear imprints of the females' pygidial plates. Although there was no clear evidence of a masoned wall, such walls probably would have been undetected because of the fine-grained nature of the substrate. Laterals leading to cells descended obliquely downward and were filled after cell closure.

Cells, arranged singly, had their long axis varying in orientation from vertical to about 45 degrees from horizontal, the closure end always higher than the cell rear. Their shape

corresponded to that of *Exomlopsis solidaginis,* with a maximum diameter of 4.2 to 4.6 mm (eight measurements); length 7.8 to 8.5 mm (six measurements); and closure diameter 2.3 to 2.8 mm (eight measurements), as observed from inside the cell. In several cases there was some indication of a built-in (i.e., masoned or plastered) wall, although this feature was difficult to detect in the fine-grained substrate. The cell lining was clear, shiny, and waterproof and embossings from the female's pygidial plate were in evidence to a greater or lesser extent, particularly toward the top of the cell. The wall immediately next to the closure seemed somewhat rough in many instances, compared with the cells of other *Exomalopsis.*

The inner face of the closure was a nonwaterproof concave spiral of about four coils that were almost indistinct toward the middle. One closure was observed to have a waterproof, concave surface on the outside, indicating that this species agrees with other *Exomalopsis* regarding this feature. Instead of being completely smooth this surface bore markings of the female's pygidial plate.

PROVISIONING: A number of open cells (fig. 27) contained quantities of fluffy, loose pale pollen that seemed far more copious and less compact than the preliminary stores of *E. solidaginis.* Such masses seemed to occupy half the cell and were moist only below. All completed food loaves were composed of pale, large-grained pollen of *Sida.* They were shaped by the females into elongate loaves (fig. 28), 4.3 to 5.2 mm long (seven measurements), 3.3 to 3.75 mm in horizontal width (seven measurements) and 2.4 to 2.7 mm high (three measurements). The loaf in each case had a distinct, moderate-sized foot at the front end that, at least in several cases, touched the cell floor. The loaf was mealy and moist throughout, slightly sweet to taste and had a smooth surface. The rounded rear of the food mass was fitted to the cell rear as is characteristic in the genus.

DEVELOPMENT: White, curved, and shiny, the eggs (fig. 28) were placed on the top front of food loaves in the midsagittal plane of the cell. Two measured 2.2 to 2.3 mm long and 0.45 mm in maximum diameter. Young larvae crawled over the food surface as they fed, gradually reducing the size of the mass, but the coarse nature of the pollen obscured channeling trails, although the mass developed a somewhat uneven surface. Several older larvae were encountered circling the food loaves that were now detached from the cell rear, so that the provisions no longer contacted the cell surface. Hence, the food was held away from the feces after the larva started defecation. Some of these food loaves were ovoid, but apparently later became dumbell-shaped as the larvae became larger. Detaching of the mass took place before defecation, but soon afterward the larva, while still feeding, started to defecate.

In the case of larvae developing in late summer (see below), the feces were applied as yellow smudges on the entire cell surface. The larva then applied silk on the thin layer of feces. In the early stages of cocoon construction the silk consisted of distinct strands running in all directions and adhering to the feces, with many fenestrations in the fabric. When completed, the cocoon (fig. 29) over most of the cell surface was thin, slightly tan, semitransparent, nonfenestrated, fine-fibered, parchment-like material with a shiny but uneven (crinkly) inner surface (i.e., facing the cocoon lumen) and with an outer surface to which fecal pollen adhered. Only toward the closure (top) end was the cocoon more complex (figs. 29, 30). Here it was thicker, approximately 1 mm thick at the closure itself, and was composed of perhaps two or three layers of pollen-laden feces separated by layers of silk. As a uniform feature, the innermost layer of fecal material consisted of an opaque white, amorphous, fine-grained material (fig. 30) that contrasted with the tanner, granular feces elsewhere in the cell. This white blotch had an uneven outline, roughly the diameter of the closure, and rested on the inside of the normal pollen-laden feces at the front end of the cell. In some cases it seemed to be covered by a nearly transparent, adhering sheet of silk, and in other cases it may have been partly or completely exposed to the cell lumen. The completed cocoon, when extracted from the soil, was fragile in appearance and collapsed easily except at the front end where the layers of feces and silk provided a firmer structure. Larvae in the cocoons (fig. 29) were quiescent, pale overwintering forms, curled on their backs with

their heads somewhat lower than the tips of the abdomens.

Although all fully fed larvae encountered on September 3 were either spinning or had spun cocoons (table 1) as described above, no individuals of the previous generation had spun cocoons. This is known because on August 29, eight active and developing pupae of the previous generation were recovered from cells (fig. 31) that had no cocoons and in which the feces were plastered against the bottom (rear) of the cell in a mass of flat, elongate tannish pellets that extended as streaks approximately two-thirds up the cell wall. In all cases, most of the feces were at the bottom of the cell and the amorphous, opaque, white, nongranular substance was the innermost material, the last to be deposited. The cast larval skin, with its characteristic mandibles, could usually be identified adhering to the white material or to the tan feces. In the nests excavated on September 3, adults of the first generation had emerged, but their vacated cells, now filled with soil, revealed the feces, larval skins, and no cocoons.

Hence, it seems clear that one generation did not spin cocoons, whereas the subsequent one did. This phenomenon was suggested earlier by Rozen, Eickwort, and Eickwort (1978) with respect to *Protepeolus singularis.* In the case of *Exomalopsis sidae,* the noncocoon-spinning generation probably occurs in spring or early summer, and the cocoon-spinning generation apparently overwinters as quiescent larvae in cocoons. Surprising is the marked difference in placement of the fecal material in the two generations—at the bottom and lower sides of the cell in the earlier generation, and mostly at the top but also totally covering the entire cell surface in the late summer, overwintering generations. The importance of the cocoons for overwintering larvae is unknown.

Postdefecating larvae of the noncocoon-spinning generation were not observed. It is unknown, therefore, whether they had projecting salivary lips and labiomaxillary regions characteristic of cocoon spinners, or whether they lacked such projecting adaptations. Although seasonal larval dimorphism seems unlikely, this matter should be investigated.

Vacated cells of previous generations as well as cells currently occupied were uncovered, indicating that the three nests were used by more than one generation.

ADULT ACTIVITY: Adults were active during my three visits to the site. Peak activity seemed to be late morning, but many individuals were still flying in midafternoon. Foraging females flew rapidly from flower to flower. Males flew in a similar fashion, probably in search of females in flowers. Male flights were swift, not the slow deliberate flight of certain other *Exomalopsis.*

PARASITISM: Only a single male of *Melanomada sidaefloris* was seen flying over the flowers during the three days of observation, excavation, and collecting, and only a single female[8] was collected, as it emerged from a nest. In spite of the lack of adults of this parasitic bee, the cells of *Exomalopsis sidae* were heavily parasitized by this species (see table 1).

Whereas *Exomalopsis sidae* appeared to have two generations a year, the number of annual generations for *Melanomada sidaefloris* was not clear, nor was the time phasing of the parasite population with that of the host. A possibly related problem that needs explanation was the low number of adult *Melanomada* compared with the high rate of parasitism, as revealed by immatures in the nests.

Two oviposition sites of *Melanomada* were found in cells of *Exomalopsis sidae* that already contained postdefecating *Melanomada* larvae. Each was a hinged flap of cell lining and wall, as is characteristic of the Nomadini (Rozen, 1977b), found halfway from the rear of the cell to the closure. Active *Melanomada* larvae were found in various positions on the loaf, indicating that they moved while feeding. Postdefecating larvae (fig. 32), rigid, white, and without cocoons, were invariably found with the anterior end closest to the cell closure. The feces had been plastered to the rear (bottom) of the cells, as elongate partly

[8] This female agreed with those *Melanomada* females associated with *Exomalopsis consobrina* (Rozen, 1977b) except that the integument of its head, mesosoma, and appendages was somewhat blacker. The first flagellar segment was nearly concolorous with the other segments, rather than distinctly redder as was the case with the *consobrina* associates. Its clypeus was also somewhat more densely punctate. Until more individuals associated with both host bees can be examined, these *Melanomada* will be considered conspecific.

TABLE 1
Collection of Immatures of *Exomalopsis sidae* and *Melanomada sidaefloris*[a] on Two Different Dates in 1983

	August 29		September 3	
IMMATURES	*Exomalopsis sidae*	*Melanomada sidaefloris*	*Exomalopsis sidae*	*Melanomada sidaefloris*
Pupae	8	1[b]	0	0
Postdefecating larvae	0	2	18	8
Postfeeding larvae	1	1	1	4
Feeding larvae				
Large	0	2	5	2
Intermediate	0	1	2	0
Small	1	1	9	0
Eggs	2	0	1	0
Total	12	8	36	14

[a] (See footnote, p. 20.)

[b] This pupa remained alive but inactive and did not develop in contrast with the pupae of *Exomalopsis sidae* collected at the same time and which were active and developed rapidly.

fused pellets that extended roughly halfway to the cell closure.

Eremapis parvula Ogloblin

Neff (in press) treated many aspects of the nests of this Argentinian species, the only one in the genus *Eremapis,* and compared its biology with that of other exomalopsines.

Ancyloscelis apiformis (Fabricius)[9]

Aspects of the nesting biology of this species have been treated in considerable detail by Torchio (1974) and Michener (1974a), under the name of *Ancyloscelis armata* (Smith), and briefly by Linsley, MacSwain, and Michener (1980). Brèthes (1909) also commented on the nests of this species. Although my observations parallel theirs in most respects, new information and, in certain instances, information that seems to disagree with their observations, warrant yet another review of the biology of this species.

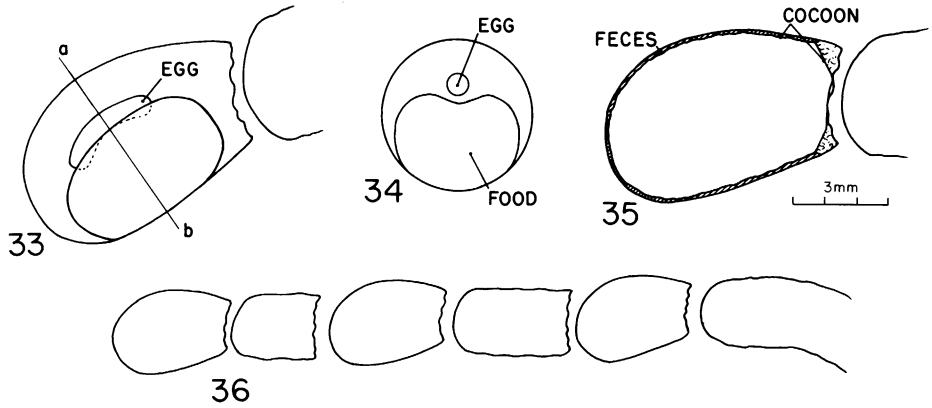
DESCRIPTION OF NESTING AREA: Nests of this species occurred in a 10-m section of a vertical bank that extended for 30 m along a paved roadway in Maracas Valley, Trinidad. The site was studied by me and Dr. F. D. Bennett, who had discovered it in late February and early March 1966, and again by me and Barbara Rozen in early March 1968. Three to 4 m high, the bank was without vegetation at the nest area, although elsewhere it was partly covered with plants. The lower level was sand intermixed with large rocks, whereas the upper level, where most nests occurred, consisted of an even, fine-grained orange sand that was so hard and compact that it had to be chipped with a hunting knife to be excavated. The bees were common here but not elsewhere. They may have chosen this site because it lacked any sign of moisture, unlike most roadside embankments on Trinidad in late February and early March. The bank faced south and was exposed to the sun during most of the day. Intermixed with numerous nests of this species were a great many of *Melitoma segmentaria* (Fabricius),[10] although most of these were inactive.

NESTING ACTIVITY: Although numerous females of *Ancyloscelis apiformis* and one of *Melitoma segmentaria* were transporting pollen to their nests, plants of the genus *Ipomoea,* to which both genera are restricted, were not noticed in the vicinity of the nesting area.[11] Nest entrances of both species in 1968

[9] Identified by J. G. Rozen, Jr.

[10] Identified by Dr. Thomas J. Zavortink.

[11] John L. Neff (*in litt.*) informed me that *Ancyloscelis apiformis* "collects both *Ipomoea* and *Convolvulus* pollen in Texas and some of the odd *Ancyloscelis* with hooked hairs on the mouthparts are apparently restricted to the Pontederiaceae."



FIGS. 33–36. *Ancyloscelis apiformis.* 33. Cell with egg and food loaf, side view. 34. Same, showing food and egg in cross section at line *ab* in figure 33. 35. Cell, side view, showing cocoon and feces. 36. Three cells in series, separated by short tunnels. Scale refers to figures 33–35.

seemed to be most abundant in the 10 to 15 cm deep excavations made by us in the face of the embankment in 1966. These depressions had existed for two years without appreciable change, a fact signifying the permanency of the bank face. Torchio's nests (1974) from Mexico came from a vertical adobe wall that was "completely honeycombed" with old burrows and cells of two species, *A. apiformis* and *Melitoma* sp.,[12] a situation that closely parallels the Trinidadian nesting site. Michener's nesting area, "a small cave under a huge rock" near the Universidad del Valle in Cali, Colombia, was inhabited by "probably the same two anthophorines." However, Michener could not be absolutely certain that the *Ancyloscelis* was *apiformis* because of the lack of males. His nest site differed from mine and probably Torchio's because it was in "deep shade."

Michener suggested that the association of *Ancyloscelis* and *Melitoma* might be because "*Melitoma* plays a significant role in preparing a site for later occupancy by *Ancyloscelis.*" Although a reasonable hypothesis, no facts other than dual site occupancy suggest this. Such occupancy could as easily be a concordance of nesting requirements involving dry vertical banks near their common food source, *Ipomoea.* The fact that *Ancyloscelis* females sometimes construct their own burrows, as shown by both my observations and those of Michener, indicates that *Ancyloscelis* is quite independent from *Melitoma* so far as any need to use another bee's burrow to start its own. Further observations may shed more light on this interesting microdistributional overlap.

Because so many twisting and anastomosing burrows, both new and old, occurred in the nest area, we could not excavate a single nest so as to learn its form, as also was the case for Torchio's study (1974). Only Michener (1974a) gave a nest diagram. In Trinidad females of *A. apiformis* carrying provisions entered not only *Ancyloscelis* burrows (about 3.0 to 4.0 mm in diameter) but also the considerably larger (5.5 mm) ones of *M. segmentaria.* The entrances constructed by *Ancyloscelis* were both on the vertical cliff and also under the overhang where we had made excavations in 1966. These entrances lacked turrets, and the walls of the main burrows were moderately rough with no indication of a soil lining as found in some tunnels by Torchio (1974), and with no evidence of liquid having been used by the females to soften the soil during construction. Because *Ancyloscelis* entered only those *Melitoma* burrows that had no turrets, they were probably reusing vacated burrows of *Melitoma. Ancyloscelis* females were also seen entering nests of previous generations of *Ancyloscelis,* as well

[12] Linsley, MacSwain, and Michener (1980) identified this *Melitoma* as *marginella* (Cresson).

as fresh ones. All tunnels were open except for some that were blocked by thin septa; none was filled with soil.

Contrary to Michener's observation that new cells are attached to previously occupied ones, *Ancyloscelis* in Trinidad probably did not construct cells along old tunnels, be they of *Ancyloscelis* or *Melitoma,* because current cells always seemed to be attached to fresh *Ancyloscelis* burrows. Old nests of *Ancyloscelis* could be recognized immediately because the sand surrounding them was darkly stained, whereas no stain was seen in the vicinity of new burrows or cells. *Ancyloscelis* did not wall-off parts of old burrows or fill-in tunnels that were too large, as did *Exomalopsis chionura* (Rozen and MacNeill, 1957). However, Torchio (1974) reported that cell walls were sometimes partly built into old cells.

Cell orientation in the nest of *A. apiformis* varied from nearly horizontal to almost vertical, in agreement with the observations of both Torchio and Michener. The front of most but not all cells was as high or higher than the rear. Cells arranged singly were connected to an unlined lateral about 7 mm long; at least some of these laterals were walled off from the main burrow by a septum. Most cells were in series of two or three, and were either directly connected to one another, or, more often, were separated by sections of tunnel, 5 to 7 mm long (fig. 36), the walls of which were not waterproof. These facts corroborate Torchio's observations, except I am uncertain that the tunnels between cells are "generally filled with loose soil."

Slightly flattened on the lower side, the cells (fig. 33) were about 7.0 mm long and 4.5 to 4.8 mm in maximum diameter (four measurements), figures that correspond with those of Michener and are slightly less than Torchio's. At the closure, the cells ranged from 3.0 to 3.5 mm in diameter, somewhat less than the diameter of the tunnel. The cell wall was smooth, more so than the tunnel walls or connecting burrows (but not quite as smooth as the inner surface of the *Melitoma* cells), and was not obviously made of soil mixed with some secretion, as seemed to be the case with *M. segmentaria.* The inner cell surface was the same color as the matrix, and lined with a varnish-like material that imparted a faint shine. The glistening effect was enhanced by placing a small fragment on a hot plate at 700°F. where the lining darkened but did not char. Another fragment of cell lining with substrate attached was placed in water, resulting in the substrate "melting away," leaving the curved cell lining undissolved with the adhering soil particles attached. This remaining lining was nearly as thick as the larger soil particles. These observations seemingly disagree with those of Torchio (1974), who stated that the inner cell layer was composed of "small, tightly appressed soil particles" and "not coated with secreted materials nor were secretions incorporated into it." The coating was presumably responsible for waterproofing the cell; a droplet of water placed on the wall was very slowly absorbed. Other details of cell construction given by Torchio are difficult to relate to my observations. Further study is needed to reconcile these matters.

After the cell was provisioned, it was closed with a moistened thin plug of soil that subsequently dried. The closure (fig. 33) on the inside was a distinct spiral that was flat or, more often, slightly convex, in contrast to the concave cell closures of most bees. The outer surface of the plug was very smooth and concave, and showed no indication of a spiral, whether or not it formed the rear of the next cell in the series. Several closures measured 0.5 to 1.5 mm thick at the middle. Closures seemed to be water absorbent on the inside, but more or less waterproof on the smooth outer face. Cells were constructed only a short distance into the bank, the deepest not penetrating much beyond 10 cm.

PROVISIONING: Females of *Ancyloscelis apiformis* transported the pollen dry to the cell. Apparently the pollen was then mixed with nectar, and placed in a slightly moist, fluffy condition at the rear of the cell. When a sufficient quantity was accumulated, the female added considerably more liquid, and shaped it into an elongate loaf (fig. 33) that was no longer fluffy. This light tan food mass resting on the floor of the cell was homogeneously mealy, and 5.0 to 5.5 mm long, 3.75 to 4.0 mm in maximum width, and 3.0 to 4.0 mm in maximum height (three measurements). Occupying a large part of the cell (fig. 33), the front part of the mass was slightly

higher than the rear, and the top surface was broadly grooved longitudinally (fig. 34). The provisions lacked a "foot" (Rozen and MacNeill, 1957).

DEVELOPMENT: The slightly curved egg (fig. 33) was placed in the midsagittal plane of the cell on the top surface of the loaf, so that it rested in the groove. As indicated by Torchio, but contrary to Michener's observations, some eggs (fig. 33) were situated on the middle of the top; others, more toward the rear. The anterior and posterior ends of the egg touched the pollen mass, and the middle part curved upward; neither end was firmly attached to the provisions. Measuring approximately 3.0 mm long and 0.7 mm at maximum width, the egg had a smooth transparent chorion that lacked sculpturing. The collapsed chorion remained behind when the larva emerged and crawled away.

We did not make detailed observations on the larval instars and their activities. However, the elongate young larvae moved about the pollen mass while they fed and were found both on top of and underneath the food loaf. As the larva fed, the pollen mass became smaller but was not obviously channeled. However, Torchio found that in Mexico the food loaves were channeled by the feeding activity of the larva.

Larvae started defecating considerably before the provisions were totally consumed; one larva was defecating while one-fourth to one-third of the food remained. Feces were extruded as elongate pellets consisting of partly collapsed pollen grains. The pellets, about 0.5 mm long, were smaller than those of most bees. Feces (fig. 35) were rather evenly appressed to the floor, roof, and side of the cell but were not attached to the cell closure or to the wall near it, just as described by Torchio.

When the still-active larva completed defecating, it spun a cocoon (fig. 35) first by attaching silk to the feces, then adding more silk to the feces, while at the same time, spinning a cap near the cell closure. This cap was not firmly attached to the closure and usually just touched it near the middle, whereas the rest of the cocoon could scarcely be separated from the excrement. The finished cocoon was thin, semitransparent, light tan, and consisted of a single layer: that is, fecal material was not sandwiched between layers of silk. These features were also observed by Torchio.

The larva was oriented in the cocoon with its anterior end closest to the closure. Although some larvae were found resting on their sides, most rested on their dorsa. At least some such larvae were totally quiescent and flaccid. Pupae were usually found resting on their dorsa with their heads closest to the cell closures.

As all stages (eggs, larvae, pupae, and adults) were found at the same time, *A. apiformis* may have numerous generations a year; whether or not there is a seasonal inactive period is unknown.

PARASITISM: No parasitic bees were associated with the nesting site nor were meloids or mutillids encountered. The commonest possible parasites were adult leucospids which flew in a dancing fashion along the embankment, although none was found in the cells. Walls and closures of many old cells had been bored by some small creature, perhaps an ant, and the contents removed, but none was encountered during our observations.

Ancyloscelis panamensis Michener

Nests of the species were discovered and described by Michener (1954).

ANALYSIS OF THE NESTING BIOLOGY OF THE EXOMALOPSINI

This section summarizes my observations and those reported in the literature, on the nesting behavior of exomalopsine bees. It is intended to provide an overview of their behavior and to identify areas where knowledge is lacking so that future studies can be more focused, especially for data of phylogenetic significance. Although our knowledge of these bees has increased over the last 25 years because of interest in bee behavior, the following account is based on only 13 of the 26 genera and subgenera assigned to the tribe by Michener and Moure (1957) and Toro (1976). Information discussed below has been presented for the first time under the appropriate species heading in the foregoing section, or the references to it can be found there.

CHOICE OF NESTING SITE: The Exomalopsini appear to be predominantly ground nesting with only *Paratetrapedia gigantea* having

been discovered nesting in a fallen dead tree.[13] The surface slope of nest sites varies considerably. Both species of *Tapinotaspis, Eremapis parvula,* and all *Exomalopsis* burrowed into slightly sloping to horizontal ground (even though females of *E. chionura* descended into cracks rather than burrows, in a gently sloping surface before digging more or less horizontally). A nest of *Monoeca schrottkyi* was reported in a vertical surface, and, although I found *Monoeca lanei* nesting on a horizontal path, the entrances were at the edge of the path where it rose to the surrounding field, a condition which might be interpreted as vertical or at least strongly inclined. *Lanthanomelissa* burrowed into a vertical surface. Such surfaces were also the choice of *Ancyloscelis apiformis* in six widely separated localities, but a flat sandy clay floor protected by the roof in an abandoned house was used at another locality (Linsley, MacSwain, and Michener, 1980). *Ancyloscelis panamensis* nested in slightly sloping ground.

To what extent exomalopsines prefer barren ground to a vegetated surface is not altogether clear. Although nest entrances in barren or sparsely vegetated ground are easier for the researcher to find, the great number of observations recorded here suggest that most exomalopsines prefer barren or semibarren nest sites. One notable exception was *Tapinotaspis tucumana,* a number of nests of which were found in dense, low vegetation. Numerous nests of *Ancyloscelis panamensis* were partly hidden in grass.

SOCIAL ORGANIZATION: A considerable diversity exists among exomalopsines with respect (1) to solitary versus gregarious nest associations; (2) to parasocial (*sensu* Michener, 1974b) as opposed to solitary nesting behavior; and (3) to the continued use of nest areas or even nests from one generation to the next. The following species nest in loose or tight aggregations: *Paratetrapedia oligotricha, Tapinotaspis caerulea* (Vogel, 1974), *Exomalopsis globosa, similis, chionura,* perhaps *sidae, crenulata, Eremapis parvula, Ancyloscelis apiformis* (Torchio, 1974; Michener, 1974a; and present paper), and *Ancyloscelis panamensis.*

With other species, either only isolated nests have been found or nests seem widely dispersed as opposed to being aggregated. These are: *Tapinotaspis tucumana, Exomalopsis aureopilosa,* perhaps *solidaginis,* probably *compactula,* and *consobrina.*

The underlying adaptive basis (or bases) for nesting in aggregations or singly is not understood in any of these cases and seems to have little phylogenetic significance because both behavior patterns exist in *Exomalopsis* and *Tapinotaspis,* and because even within *Exomalopsis* both patterns occur within the subgenera *Anthophorisca* and *Exomalopsis sensu stricto.*

Communal nesting behavior, that is, more than one female actively occupying a nest, is well documented in the tribe. Claude-Joseph (1926) recorded numerous females in a nest of *Tapinotaspis caerulea,* and Vogel (1974) also indicated that there may be more than one female to a nest of the same species. All observed species of *Exomalopsis* seemed to have more than one female to a nest, and a nest of *E. aureopilosa* contained 884 females. On the other hand, species in other genera are known to have only a single female to the nest, including *Paratetrapedia oligotricha, Tapinotaspis tucumana,* and *Monoeca lanei. Ancyloscelis panamensis* seems to have but a single cell to a nest as was also suggested for *Eremapis parvula* (Neff, *in litt.*).

Several workers have investigated the social relationships among adults in *Exomalopsis* nests. Michener (1966) concluded that females of *Exomalopsis solani* provisioned cooperatively because foragers with undeveloped ovaries as well as those with developed ovaries collected pollen. Raw (1977) decided that both *Exomalopsis globosa* and *E. similis* were at least quasisocial because more pollen gatherers inhabited a nest than there were cells being built and provisioned. He further concluded that these bees were possibly semisocial, because the large proportion of foragers with vestigial oöcytes suggested a division of labor with respect to egg layers

[13] Robert W. Brooks (*in litt.*), who kindly read this manuscript, has noted that some *Paratetrapedia* (*Paratetrapedia*) and *P.* (*Lophopedia*) have "tridentate mandibles which may be related to wood nesting." He "saw *P.* (*Paratetrapedia*) *lugubris* Cresson nesting in a leafcutter bee (*Megachile rotundata*) trapnest and also in what appeared to be beetle burrows in April 1981 at Curundu (Panama Province), Panama."

and nonegg layers in a nest. He surmised that nests were started by a few females because two and three females per nest were discovered in nests from which no bees had yet emerged. He noted that "the numbers of adult bees in the larger *Exomalopsis* nests were very similar to the numbers of cells in them from which bees had emerged, which suggests that most of the emerging bees were females and that they remained associated with their natal nest, forming sister colonies."

Occupation of a nesting site, or of even a single nest, for more than one generation, as evidenced by the presence of numerous vacated cells, has been observed in a number of species all of which (with the possible exception of *Ancyloscelis apiformis*) are communal: *Tapinotaspis caerulea* (Vogel, 1974), *Exomalopsis aureopilosa, globosa, similis, solidaginis, compactula, crenulata, chionura, consobrina, sidae,* and *Ancyloscelis apiformis.* The data suggest that communal bees tend to occupy nest sites and nests for more than one generation.

NEST STRUCTURE: Considerable information exists on the nest elements of exomalopsines, which, except for *Paratetrapedia gigantea,* are known to nest in the ground. Among exomalopsines, only *Monoeca lanei* has been recorded to construct turrets around nest entrances. The adaptive and phylogenetic significance of turrets in this species (situation not recorded for *Monoeca* species, or *M. schrottkyi*) is unknown, but some melitomines and anthophorines do build distinct turrets.

Exomalopsis chionura, crenulata, compactula, perhaps *solidaginis, Ancyloscelis apiformis* (Torchio, 1974), and probably other exomalopsines at times line burrows with soil that is different in consistency or particle size from the surrounding substrate. In some cases, this lining appears to be an attempt on the part of the female bee to wall-off other bee burrows or cells that are too large or perhaps in other ways unsuitable. To what extent this is in the common repertoire of behavior patterns for the tribe is unknown. In the few cases where it has been identified, it seems that this type of lining does not retard the absorption of water droplets. In one case (*Monoeca lanei*), the burrows as well as the cells were lined with a waxy material that retarded the absorption of water droplets. This appears akin to the waterproof lining of the cells, and is very different from plastered walls.

In general, available data do not reveal great differences among taxa with respect to nest configuration except as noted below. So far as is known, all nest entrances and main tunnels remain open during nest construction and provisioning. Laterals leading to completed cells are filled or partly filled with soil. Nest patterns for all representatives seem to consist of a main tunnel, which may (*Exomalopsis*) or may not (*Tapinotaspis tucumana*) branch many times, with laterals extending variable distances to cells. The main tunnel often is vertical, sometimes straight, but more often somewhat meandering in those species that nest in horizontal or nearly horizontal surfaces. Nests built into vertical banks tend to have the main burrow and branches essentially horizontal (*Paratetrapedia oligotricha*; *Lanthanomelissa* species; and *Ancyloscelis apiformis,* Michener, 1974a). Depths of nests vary considerably. Perhaps *E. aureopilosa* has the deepest nest of any known bee, recorded at 5.3 m. As one would expect, this large (deep) nest was correlated with adult population size: it was inhabited by 884 females and 46 males. Of the 15 species for which we have information, only *Ancyloscelis panamensis* appears to construct but a single cell to a nest. Its close relative, *A. apiformis,* clearly has numerous cells to a nest.

Although few differences can be detected in general nest pattern within the tribe, cell features vary considerably and give promise for further analysis. Most species arrange cells singly at the end of laterals, but linear series of cells are constructed by some species. According to Claude-Joseph (1926), *Tapinotaspis caerulea* excavates cells in series, although Vogel (1974) claims that cells of this species are arranged singly. *Exomalopsis chionura* builds cells both singly and in series, and *Ancyloscelis apiformis* usually but not invariably has cells in series, with individual cells of a sequence often being separated by sections of tunnel.

Cell orientation, that is, angle of the "long axis" of the cell to the horizontal, is extremely variable. Some species have uniform cell orientation, which may be horizontal (*Exo-*

malopsis similis, Eremapis parvula); slightly inclined (20 to 30 degrees) toward the rear (*Tapinotaspis tucumana, Exomalopsis compactula*); considerably inclined (30 to 45 degrees) toward the rear (*Exomalopsis globosa, consobrina*); or vertical (*Paratetrapedia oligotricha, Exomalopsis aureopilosa, Monoeca lanei, Monoeca* species). With other species cell inclination may vary from horizontal to vertical in a single nest, as in *Exomalopsis chionura, solidaginis,* and *Ancyloscelis apiformis.* Considering the variation in cell orientation, one must ask the question, why are some species behaviorally locked into a fixed orientation of their cells, whereas other species are quite variable in this regard? The great range of variation within the genus *Exomalopsis* seems to suggest that cell orientation is not a significant feature for phylogenetic interpretation.

Information on cell shape for exomalopsines is sketchy: (1) because of difficulties in analyzing and describing cells, even in the best of circumstances; (2) because cells are normally extracted from the ground as broken fragments that are difficult to reassemble; (3) because cell shapes are often complicated; and (4) because observers often tend not to examine cells closely under a microscope. Cells described in the present paper were observed through a stereoscopic microscope, in the field, in the laboratory, or in both. These cells are not symmetrical around a straight longitudinal axis. With cells that are not vertical, the lower surface (floor) is flatter than the upper surface (ceiling), which is therefore slightly more vaulted, all as seen in longitudinal section. Such shapes appear to be characteristic of *Tapinotaspis tucumana,* species of *Exomalopsis* described herein, and *Ancyloscelis apiformis.* Vertical cells, at least of *Monoeca lanei,* also seem to be slightly flatter on one side than the other, so that this feature may be characteristic of the Exomalopsini irrespective of cell orientation.

In a number of taxa (*Exomalopsis chionura, compactula, crenulata, Ancyloscelis apiformis,* Torchio, 1974), the female constructs the cell first by making a cavity in the soil and then by plastering its surface with a mixture of fine soil mixed with some other substance, perhaps a secretion, so that the surface of the cell wall is smooth and fine grained. In certain other species (*Exomalopsis chionura* and *Ancyloscelis apiformis*) there is clear evidence that old cells and burrows can be walled-off with the cement-like material. With other taxa, there is no information about a specially formed plaster wall (*Tapinotaspis tucumana, Monoeca lanei, Exomalopsis solani,* and *consobrina*). Although I noted no plaster cell wall with *Ancyloscelis apiformis,* Torchio (1974) clearly noted such a wall. This suggests either that a species may construct such a wall only under certain circumstances, or, more likely, that plastered walls can be easily detected when there is a marked difference between the texture of the substrate and the fine-grained cement-like material. This is not to say, however, that all exomalopsines construct masoned walls. Data are lacking to draw such conclusions. Female exomalopsines apply a very thin coating of a transparent or semitransparent, smooth, shiny material on the cell wall. This film probably accounts, in all cases, for the waterproof nature of the inner surface of cells, although the waterproof nature of the plastered part of the cell walls has yet to be tested. The only noted exception (Parker, in press), recorded that droplets of water were quickly absorbed by the cell wall of *Exomalopsis crenulata.* In most cases tested, this lining was nonwaxlike in that it did not melt even at temperatures of 700°F. However, the cell lining of *Monoeca lanei* did melt, somewhat below the boiling point of water, when I tested it. Similarly, Vogel (1974) reported that the cell lining of *Tapinotaspis caerulea* melted when heated. He also noted that the lining became opaque, presumably when the cell dried out, which is also characteristic of *Monoeca lanei.* In contrast, the cell linings of the presumably related *Tapinotaspis tucumana* did not melt when heated. Zucchi (1973) claimed that the cells of *Exomalopsis aureopilosa* were coated with a waxy layer produced by glands associated with metasomal terga IV through VI. These rather profound differences do not correlate well with the presumed relationships of these exomalopsine taxa, and therefore raise questions that warrant further study. It is clear from investigations of Batra (1972) and Cane (1983) that the chemistry of cell lining in bees is far more complicated than bee specialists had thought

heretofore, and that sophisticated chemical analysis will yield considerable new information.

Cell closures in Exomalopsini are apparently invariably spiraled on the inside, that is, the side of the plug facing the cell lumen. Spiral closures are characteristic of many diverse groups of bees (Apoidea) and are found in the following families: Colletidae (Rozen, 1984); Stenotritidae (Houston, 1975); Oxaeidae [New Information]; Andrenidae (Malyshev, 1935); Halictidae (Torchio et al., 1967); Melittidae (Malyshev, 1935); Ctenoplectridae (Rozen, 1978); and Anthophoridae (Malyshev, 1935). Spiral closures to cells have not been recorded for the Megachilidae (including the Fideliinae) (Rozen, 1977a) except in one case (Rust, Thorp, and Torchio, 1974) and Apidae (Malyshev, 1935). If this is indeed the case, then the nonspiral closures such as found in *Halictus sensu lato* (Malyshev, 1935), most Megachilidae (Rozen, 1977a), *Colletes* (Malyshev, 1935), and Apidae, are independently derived apomorphic traits.

Although the spiral nature of the closures is characteristic of the tribe, other aspects of the closures vary. For bees in general, most such closures are conspicuously concave on the inside. This is also true within the tribe for *Tapinotaspis tucumana, Monoeca lanei,* but not for *Ancyloscelis apiformis,* where the closure is flat or even slightly convex on the inside. Within *Exomalopsis,* in some species (*solani, solidaginis, sidae*) the spiral is concave, but in *compactula, consobrina,* and *chionura* it is flat or nearly so. The spiral closure characteristic of this tribe may be water absorbent on the inside, that is, water droplets placed on the spiral are absorbed nearly as rapidly as are water droplets placed on the substrate. This seems to be true for *Monoeca lanei, Exomalopsis solani, solidaginis, chionura, sidae,* and *Ancyloscelis apiformis.* With other taxa, the closure is more or less waterproof, when tested the same way, including *Tapinotaspis tucumana* and *E. compactula.* The reason for the retarded rates of water absorption in the case of the last two species is not understood, but it is not the result of wax or a shiny film of material covering the inner face of the closure, as is the case at least with some *Anthophora* and *Emphoropsis.*[14]

An unusual feature of the cell closure of some exomalopsines is that it has a distinct, strongly concave outside surface (fig. 18), which abuts the lateral. This surface is usually as smooth and hard as the cell wall, clearly different from the more loosely packed fill of the lateral, and apparently not absorbent to droplets of water. Such outer surfaces were detected in *Exomalopsis solani, solidaginis, compactula, chionura, sidae,* and *Ancyloscelis apiformis.* This may well prove to be characteristic of all *Exomalopsis.* Nests of *Exomalopsis chionura* and *sidae* differ from the others of the genus in that the outer surface is clearly embossed with the impressions of the female's pygidial plate, and therefore is not as smooth as the outer surfaces of closures of other species. In contrast to this type of closure is that of *Tapinotaspis tucumana* and *Monoeca lanei,* in which the soil of the closure grades into the fill of the lateral so that there is no obvious demarcation between the textures of the two substances.

The matter of gas exchange between the interior of the cell and the outside has rarely been addressed with respect to ground-nesting bees. With some taxa, the closure seems sufficiently unconsolidated to permit oxygen to enter the lumen and carbon dioxide to escape. This method of exchange seems particularly plausible in those bees in which the cocoons are more porous where they contact the cell closures. However, the cell closures of exomalopsines seem well consolidated, and therefore, not very permeable. This consolidation is characteristic of all exomalopsines on the spiral face of the closure, and in certain species, on the outer surface as well (fig. 18). This is another matter that needs further investigation.

PROVISIONING: Vogel (1974) reported that some Exomalopsini are known to provision their nests with oil and pollen rather than nectar and pollen. The oils are obtained from

[14] Philip F. Torchio (*in litt.*) after reading this manuscript wrote: "In studying *Pseudomasaris edwardsii,* I was amazed to learn how waterproof cell walls and caps became when the wasp simply added nectar (sugar) to the soil it manipulated for cell construction."

certain plants with special oil-secreting glands. More recently, Neff and Simpson (1981) surveyed the New World anthophorids with respect to oil collecting and discussed the possible roles of the floral oils in the biology of oil-collecting bees.

Foraging females returning to the nest deposit pollen loads associated with liquid (presumably oil or nectar) on the lower part of the cell (that is, the rounded rear of the cell in vertical and semivertical cells, and the floor of the cell in horizontal or nearly horizontal cells) before bringing in another load. These preliminary deposits are not shaped into the form of a preliminary loaf, at least in the case of *Tapinotaspis tucumana, Monoeca lanei, Exomalopsis globosa, similis, solidaginis, sidae,* and *Ancyloscelis apiformis.* When the female has gathered the total quantity of food, she then molds it into a form that is taxon-specific and places the completed form in a taxon-characteristic position in the cell. The shape of the form, in most cases, is loaflike, that is, with the long axis that more or less parallels that of the cell, with the top flattened and with the rear rounded and the front somewhat truncated. In some species the front end is drawn downward into a projecting foot that normally rests on the floor of the cell while the rounded rear fits into the lower rear end of the cell; hence the loaf, which has a smooth surface, touches the cell wall only at these two points. This kind of loaf is characteristic of *Exomalopsis chionura,*[15] *consobrina* (fig. 37B) and *sidae* (fig. 28). *Exomalopsis solidaginis* (fig. 20) has a similar food mass, but the foot is short and does not touch the floor, and thus the loaf is suspended only by its attachment to the rear of the cell. Although the presence of a foot in *E. solani* was uncertain, the loaf is otherwise like these species. The descriptions of the loaves of *E. globosa* and *similis* by Raw (1977) seem to suggest a shape similar to those of the other *Exomalopsis,* but the smooth food mass of *E. aureopilosa* seems quite different according to the diagrams of Zucchi (1973). Although he refers to the mass as having a "foot," this projection at the bottom (rear) of the vertical food mass in a vertical cell seems in the wrong position to be the same as the foot of other species. The elongate, shaped provisions of *Eremapis parvula,* as drawn by Neff (in press), appear similar to those of *Exomalopsis* and are attached only at the front and rear of the cell, but a foot is not shown or described. The food mass of *Ancyloscelis apiformis* is also smooth and loaflike, but it lacks a foot, its midsection is attached to the floor of the cell, and the upper surface is shallowly grooved longitudinally.

Information regarding the food masses of the other exomalopsines varies considerably. The food loaf of *Tapinotaspis tucumana* is like that of *Exomalopsis solidaginis,* in that it is apparently attached only to the rear of the cell. Fresh masses appear to have a rough surface, possibly the result of mold. However, the food of *Tapinotaspis caerulea,* as shown by Vogel (1974), also has a granular surface, although its shape (fig. 37F), a ball resting in a socket of almost liquid paste (oil) at the rear of a horizontal cell, is quite different from the loaflike mass of *Tapinotaspis tucumana,* which is also in a more or less horizontal cell. To further confuse the picture, *Monoeca lanei* has the food mass with an uneven surface "cemented" almost vertically into a somewhat more moist food mixture at the bottom of the verticle cell. Although difficult to interpret on the basis of limited information, these food masses may actually have some important similarities. The oily "socket" of *Tapinotaspis caerulea* may correspond to the soft cement of the bottom of the cell of *Monoeca lanei.*[16] Uneven, granular, and convoluted surfaces may represent different degrees of a common texture in these three taxa. Spherical shape of the main food mass of *Tapinotaspis caerulea* may be a rather extreme form of the vertical loaf of *Monoeca lanei,* and the elongate rough loaf of *Tapinotaspis tucumana* in a horizontal cell may be similar to the suspended loaf of such bees as *Exomalopsis solidaginis.* The

[15] Stephen, Bohart, and Torchio, (1969, fig. 293) incorrectly oriented the food mass in the cell of the species. The loaf is positioned in this species as diagrammed for *Exomalopsis consobrina* (Rozen, 1977b).

[16] Robert Brooks and Charles D. Michener, both of whom read the manuscript, informed me that they believe *Monoeca* to be an oil-collector.

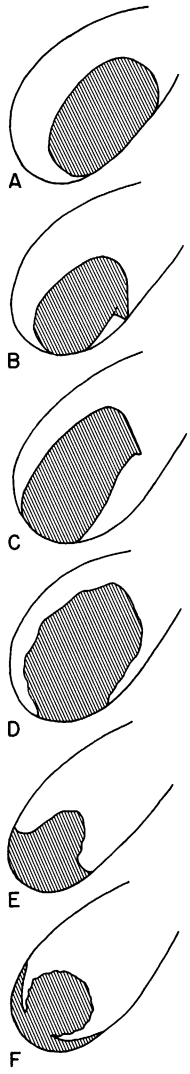


FIG. 37. Diagrammatic representation of cells and food masses of various exomalopsine bees, side view. Diagrams not drawn to same scale and all oriented at 45 degrees to aid in comparison of shape and position of food masses. This sequence is intended to show certain similarities when food masses are compared sequentially, as follows:

A. *Ancyloscelis apiformis*—smooth food mass resting on bottom of cell. B. *Exomalopsis consobrina* (after Rozen, 1977b)—smooth mass, now with front foot resting on floor of cell and with rear of mass at rear bottom of cell. C. *Exomalopsis solidaginis*—smooth food mass, still with foot but foot not resting on cell floor, so that entire mass is suspended from cell rear. D. *Tapinotaspis tucumana*—food mass now with uneven surface and without foot, but suspended from rear of cell. E. *Monoeca lanei*—food mass still uneven and aris-

topography and orientation of these masses are diagrammatically presented in figure 37. The orientation and size of the cells have been modified to aid comparison. There is no way to determine at this time if there is any phylogenetic significance to the similarities.

DEVELOPMENT: The elongate white, curved exomalopsine eggs are deposited on top of the provisions, somewhat toward the front end of the loaflike food masses, in all cases. Even the egg of *Monoeca lanei* (fig. 11), in a vertical cell, is somewhat in that position. Larvae are elongate and, so far as known, all later instars crawl while feeding (*Tapinotaspis tucumana, Monoeca lanei, Exomalopsis globosa, similis, solidaginis, chionura, sidae, Eremapis parvula,* and *Ancyloscelis apiformis*). Partly grown larvae of some taxa circle the partly consumed provisions so that the mass no longer contacts the cell wall, suggestive of the feeding habits of *Protopeolus singularis* (Rozen, Eickwort, and Eickwort, 1978). This is true for *Tapinotaspis tucumana* and *Exomalopsis solidaginis* and *sidae,* but the food mass of *Monoeca lanei* adheres to the bottom of the vertical cell until consumed.

DEFECATION AND COCOON SPINNING: Meconial material may be voided either at the beginning of the last stadium while the larva is still feeding (*Exomalopsis solidaginis, consobrina, sidae, Eremapis parvula, Ancyloscelis apiformis*) or when the food is entirely consumed (*Tapinotaspis caerulea,* Claude-Joseph, 1926; *Tapinotaspis tucumana*; *E. chionura*).[17] Where the feces are deposited in the cell depends in part on whether or not the species spins a cocoon, and in part on the species-specific pattern demonstrated by the larva. The following exomalopsines are known to spin cocoons: *Tapinotaspis caerulea* (Claude-Joseph, 1926), *Exomalopsis*

[17] This observation needs to be verified for *E. chionura* because of the more recent information regarding other members of the genus.

←
ing from rear of cell, but now embedded in softer food material. F. *Tapinotaspis caerulea* (after Vogel, 1974), food mass with uneven surface attached to socket-like softer food material at rear of cell.

similis, globosa, apparently *compactula, crenulata, consobrina, Eremapis parvula,* and *Ancyloscelis apiformis.* The following species are known not to spin cocoons: *Tapinotaspis tucumana, Exomalopsis aureopilosa, solani,* and *solidaginis.* As reported by Rozen and MacNeill (1957), some individuals of *Exomalopsis chionura* from the same nesting site produced cocoons, whereas others did not.

In *Exomalopsis sidae,* one generation does not spin cocoons and is followed by a late summer generation that produces cocoons in which the postdefecating larvae diapause, presumably for winter. A similar situation has been reported for *Protepeolus singularis* (Rozen, Eickwort, and Eickwort, 1978) and may be widespread (although not universal) in anthophorids that have more than one generation a year. For example, among the Exomalopsini, *Tapinotaspis tucumana* had well-developed salivary lips although it did not spin a cocoon but rather pupated after defecating as did the earlier generation of *E. sidae.* The discovery that some *Exomalopsis chionura* spin and some do not may actually be the result of excavating a nesting site of a multivoltine species just as it was entering its terminal generation for the year.

Exomalopsine larvae that spin cocoons have their labiomaxillary regions strongly projecting, with elongate maxillary and labial palps, and with the salivary lips produced. *Tapinotaspis tucumana* and those individuals of *Exomalopsis chionura* that do not spin cocoons also have these modifications. The salivary lips of *Exomalopsis solani* are slightly produced, even though the species did not spin a cocoon. The last instar of *Monoeca lanei* has well-developed lips, although its cocoon-spinning habits are unknown. The last stage larvae of *Exomalopsis solidaginis,* which do not spin, have recessed labiomaxillary regions. So far as I now know, larvae of a single species are not dimorphic, i.e., the generation that does not spin has a produced labiomaxillary region even though the other generation spins.

With forms that spin cocoons, onset of defecation precedes the first production of silk in most species. When defecation is completed and before spinning begins, all feces are situated between the cell surface and the cocoon fabric: *Ancyloscelis apiformis,* apparently *Exomalopsis compactula, crenulata,* and *Eremapis parvula.* The only record of feces being on the inside of the cocoon was by Claude-Joseph (1927) for *Tapinotaspis caerulea,* and this would signify spinning first and then defecation. Some species, however, start defecating first and then commence laying down silk at the same time, so that fecal pellets are incorporated into the cocoon fabric. This has been recorded for *Exomalopsis chionura, consobrina,* and *sidae.*

The placement of feces in the cell varies to a considerable extent, so far as we have clear information. *Tapinotaspis tucumana* (fig. 8) deposits fecal material at the upper rear end of the nearly horizontal cell, a situation strongly reminiscent of fecal deposition in the Halictidae, Andrenidae, as well as other major groups of bees. *Exomalopsis chionura* and *consobrina* apply feces over the entire cell wall and closure, more or less uniformly but not always evenly or smoothly. *Exomalopsis solidaginis,* however, applies most of the fecal material over the cell wall, with a smaller amount over the cell closure. *Exomalopsis compactula* (fig. 16) seems to place most of the feces over the cell closure and the front end of the cell, and *Ancyloscelis apiformis* (fig. 35) smears feces over the entire cell wall but does not cover the cell closure. *Eremapis parvula* smears most of the fecal material around the center of the cell, more or less parallel to the equator of the cell, forming a distinct ring. *Exomalopsis solani* and *crenulata* apply the feces over the cell wall, but information is insufficient to determine whether this also includes the cell cap.

Exomalopsis sidae has two patterns of fecal deposition, depending on whether the larva does not spin a cocoon but pupates immediately or spins a cocoon and undergoes diapause. In the former case the feces are primarily at the bottom (rear) of the cell; in the latter, they cover the cell wall and become a part of the cocoon structure at the cell closure. Such differences may be expected with other species if they have similar cocoon-spinning habits.

CUCKOO BEE ASSOCIATIONS: Table 2 lists exomalopsine species treated in this paper together with the cuckoo bees that have been associated with them. These associations are made with various degrees of confidence, as

TABLE 2
Cuckoo Bees Associated With Exomalopsini
(For explanation, see text)

Exomalopsine Species	Cuckoo Bee	Authority	Degree of Certainty of Association
Paratetrapedia (*Trigonopedia*) *oligotricha* (Moure)	—	—	—
Paratetrapedia (*Paratetrapedia*) *gigantea* (Schrottky)	—	—	—
Lanthanomelissa species	—	—	—
Tapinotaspis (*Tapinorhina*) *caerulea* (Friese)	—	—	—
Tapinotaspis (*Tapinotaspoides*) *tucumana* (Vachal)	*Parepeolus* sp.	Present paper	Probable[a]
Monoeca lanei (Moure)	—	—	—
Monoeca schrottkyi (Friese)	—	—	—
Monoeca species	—	—	—
Exomalopsis (*Exomalopsis*) *aureopilosa* Spinola	*Hypochrotaenia* (*Hypochrotaenia*), probably *tomentifera* (Ducke)	Zucchi, 1973	Certain[b]
Exomalopsis (*Exomalopsis*) *globosa* (Fabricius)	*Hypochrotaenia* (*Micronomada*) *cubensis* (Cresson) and *pilipes* (Cresson)	Raw, 1977	Highly probable[c]
Exomalopsis (*Exomalopsis*) *similis* Cresson	*Hypochrotaenia* (*Micronomada*) *cubensis* (Cresson) and *pilipes* (Cresson)	Raw, 1977	Highly probable
Exomalopsis (*Megomalopsis*) *fulvofasciata* Smith	—	—	—
Exomalopsis (*Phanomalopsis*) *solani* Cockerell	*Hypochrotaenia* (*Micronomada*) sp.	Linsley et al., 1954	Highly probable
	Paranomada velutina Linsley	Rozen, 1977b	Certain
Exomalopsis (*Phanomalopsis*) *solidaginis* Cockerell	*Paranomada californica* Linsley	Linsley, 1945	Suspected[d]
	Paranomada nitida Linsley and Michener	Present paper	Certain
Exomalopsis (*Anthophorula*) *compactula* Cockerell	*Triopasites pasitura* (Cockerell)	Cockerell, 1935	Suspected
	Triopasites penniger (Cockerell)	Rozen, 1977b	Certain
Exomalopsis (*Anthophorula*) *crenulata* Timberlake	*Hypochrotaenia* (*Micronomada*) *guturreziae* (Cockerell)	Parker, in press	Highly probable
Exomalopsis (*Anthophorula*) *torticornis* Cockerell	—	—	—
Exomalopsis (*Anthophorisca*) *chionura* Cockerell	—	—	—
Exomalopsis (*Anthophorisca*) *consobrina* Timberlake	*Melanomada sidaefloris* (Cockerell)	Rozen, 1977b	Certain
Exomalopsis (*Anthophorisca*) *nitens* Cockerell	*Hesperonomada melanantha* Linsley	Snelling, *in litt.*	Highly probable
Exomalopsis (*Anthophorisca*) *sidae* Cockerell	*Melanomada sidaefloris* (Cockerell)[e]	Present paper	Certain
Eremapis parvula Ogloblin	—	—	—
Ancyloscelis apiformis (Fabricius)	—	—	—
Ancyloscelis panamensis Michener	—	—	—

[a] Probable = 50/50 chance.
[b] Certain = immatures of cuckoo recovered from nest.
[c] Highly probable = numerous cuckoo bees seen entering nests.
[d] Suspected = some suggestion.
[e] (See footnote in discussion of *E. sidae*.)

indicated. The four separate genera of cleptoparasitic bees belonging to the Nomadini have definitely been linked to North American species of *Exomalopsis* alone: *Hypochrotaenia, Paranomada, Triopasites,* and *Melanomada.* A fifth genus, *Hesperonomada,* is probably also associated with *Exomalopsis.* I know of no other genus of host bee that has such a diversity of cleptoparasites.[18]

In conclusion, the Exomalopsini are a diverse group with respect to nesting biology. Not unexpectedly, there are biological traits that reflect the relationships of many of the taxa with one another, as for example the unity of *Exomalopsis.* However, available data are yet too scarce to be used as a major source of information for cladistic analysis. There is such diversity and incongruity of characteristics that I am left with the impressions that (1) the relationships of taxa within the tribe need further systematic evaluation and (2) the relationships of the Exomalopsini with the Melitomini, Ancylini, and, indeed, all the other so-called primitive, nonparasitic anthophorids require further investigation. The biological diversity offers promise that further accumulation of the kind of data presented here will be instrumental in resolving such relationships. Investigators should continue to excavate nests and make careful notes and detailed diagrams so that one taxon can be compared with the next. They are encouraged to use stereoscopic microscopes in the field on such subjects as cell shape and construction, cell lining, cell closure, and larval behavior. Saving cell samples, burrows, and turrets, as well as the immatures has been an invaluable source of information for this paper, and investigators are encouraged to label well and preserve such samples in museum collections. The relationships of the Exomalopsini with the diverse cleptoparasitic subfamily Nomadinae have been another focus of the study. Are there features of exomalopsine behavior that might be precursors to cleptoparasitism and thus indicate that these two taxa are sister groups? Several such traits are suggested. (1) Communal nesting, a common though not universal feature of the Exomalopsini, may constitute the first evolutionary step toward nest parasitism. Females using a single nest may lead to some of those females abandoning nest construction and foraging. Instead they oviposit in cells constructed and provisioned by their sisters. Communal nesting behavior is an uncommon phenomenon in other nonparasitic Anthophorinae; only certain Eucerini are communal (Michener, 1974b).[19] (2) All larval exomalopsines crawl while feeding, as do the larvae of the Nomadinae. Such behavior suggests a common ancestor, but of course most if not all other anthophorid larvae also crawl. (3) The fact that all five genera of the tribe Nomadini attack nests of various species of *Exomalopsis* is unusual, for I know of no other host genus of bees that has so many groups of cleptoparasites. Perhaps, in some way that is not altogether clear, these associations may be the vestiges of the early evolution of the parasitic subfamily and they reflect the idea that cleptoparasites tend to be related to their hosts (Wheeler, 1919; Bohart, 1970). Although these traits might possibly indicate a close relationship between the Exomalopsini and Nomadinae, they cannot be regarded as strong evidence of a relationship.

Other behavior traits of the Exomalopsini seem distant from those of the Nomadinae. Exomalopsines and other nonparasitic anthophorines place their eggs on the provisions; in contrast, virtually all nomadines insert their eggs in the cell wall, presumably hiding them from returning host females. First instars of the Exomalopsini (at least *Exo-*

[18] Both Charles D. Michener and Robert W. Brooks, upon reading this manuscript, raised questions regarding the distinctiveness of some of these genera.

[19] *Anthophora marginata* Smith is also communal in Jalisco, Mexico, according to Robert W. Brooks (*in litt.*).

malopsis solidaginis) remain enclosed mostly within the chorion, and only the second instars crawl away from the chorion as they feed on the stored provisions. The crawling mechanism of the early instars of exomalopsines is probably associated with the somewhat projecting abdominal sternum IX. In the Nomadinae the so-called first instar is extremely active, being able to crawl down the cell wall from the oviposition site, locate and crawl to the host egg or larva, and kill it with elongate tapering mandibles. The crawling mechanism usually, if not invariably, involves a forked pygopod-like structure arising laterally from abdominal segment X. However, in the Nomadinae, studies have not yet been made as to the number of larval instars, and there are some suggestions that the cast skin of an earlier larval instar may be left as the young larva crawls from the hidden chorion in the cell wall. More detailed studies of larval behavior and development within the Nomadinae may be helpful in shedding light on the relationships of the parasitic group with the Exomalopsini. In summation, behavioral evidence suggesting that the Exomalopsini and the Nomadinae are sister groups is limited.

PROFILE OF THE BIOLOGY OF THE EXOMALOPSINI

In several recent papers, I have provided in brief, telegraphic style the biological characterization of a particular higher taxon of bees. Although such synopses repeat much of the information that is discussed within the body of these papers, they also present the biological gestalt of the taxon involved in brief form. In the profiles of the Fideliinae (Rozen, 1977a) and Diphaglossinae (Rozen, 1984), such presentations seem reasonably successful, probably because of the distinctiveness and monophyly of the two taxa. The Exomalopsini seem more diverse and their relationships to other so-called primitive anthophorines, less clearly defined. Hence, the following lacks some of the unity of the other two synopses, although within the Exomalopsini the genus *Exomalopsis* is very distinctive.

NESTING: New World species inhabiting temperate arid to moist tropical situations. Body-size moderate to small, often robust. Individuals of some species solitary nesting, of others nesting in loose or tight aggregations. Although some species clearly noncommunal, others with numerous females to a nest; all *Exomalopsis* communal and quasisocial or possibly semisocial; nests of previous generation often reused in communal forms. Nest surfaces horizontal to vertical, almost always in ground except for *Paratetrapedia gigantea.* Nests moderately to very deep; those of communal species apparently without either turrets or tumuli; *Monoeca lanei* with distinct turret and *Eremapis parvula* and *Tapinotaspis tucumana* with tumuli. Main burrows circular in cross section; burrow walls in many *Exomalopsis* tamped by pygidial plate, at times masoned, normally water absorbent, but in the case of *Monoeca lanei,* lined with waxy, apparently secreted material that retards water absorption; main burrows open during nest construction and provisioning; laterals leading to completed cells filled or partly filled with soil. Nest pattern consisting of main tunnel, which may (*Exomalopsis*) or may not (*Tapinotaspis tucumana*) branch many times, and of laterals extending variable distances to cells; these laterals radiating from main burrow in all directions; laterals not ending blindly. Nests normally with numerous cells, but *Ancyloscelis panamensis* apparently with only single cell. Cells of most species arranged singly, but linear series present in some cases. Cells of some species with uniformly horizontal to vertical orientation, of others varying considerably in inclination; cells not symmetrical around straight longitudinal axis, usually with lower surface flatter than upper, as seen in longitudinal section; cell walls usually smooth but in some cases bearing imprints of pygidial plates, sometimes masoned; cell lining normally a thin film of transparent or semitransparent, smooth, shiny material, in almost all cases waterproof; this material normally nonwaxlike, in that it does not melt at high temperatures, but in *Monoeca lanei* and *Tapinotaspis caerulea* it melts at low temperatures; material apparently secreted by adults rather than transported from outside of nest. Cell closures invariably spiraled on

the inside; this surface concave, sometimes only shallowly concave, and sometimes essentially flat; surface normally water-absorbent, but in several species water-retardant, although not as a result of a shiny or waxy film over the spiral; outer surfaces of closure in many species a strongly concave, smooth, waterproof surface that does not grade into the fill in the connecting lateral; with some species (*Tapinotaspis tucumana* and *Moneoca lanei*) closure without concave outer surface distinct from fill.

PROVISIONING: Foraging females not shaping deposits of pollen before bringing in entire food supply; stored provisions shaped into loaflike forms, often with distinct "foot"; shape of these loaves somewhat variable and in some species attached to rear (bottom) of cell in various ways; provisions never liquid or semiliquid. Pollen sources unstudied; pollen transported on hind legs only; some species seeming to be polylectic, others oligolectic; source of liquid in provisions known to be oil rather than nectar in some taxa; oil-collecting habits need further investigation. Modification of provisions during larval development through action of yeasts or bacteria not reported and not observed.

DEVELOPMENT: Moderately elongate, curved egg, one to a cell, normally deposited on top of provisions, toward front end of loaflike food mass. Young larvae feeding while ambulating over surface of food, sometimes causing grooves in food masses; older larvae often circling provisions so that food masses no longer contact cell walls. Defecation commencing either at the beginning of last stadium while larva still feeding or just after food entirely consumed; placement of feces in cell quite variable, often species-specific, and variable within a species, depending on whether or not larva spins cocoon; feces a moist solid, exuded as elongate pellets or smears. Some species spinning cocoons, others not, and in some, overwintering generations spinning cocoon, whereas summer generation without cocoon; cocoon structure quite variable, depending on species; cocoon fabrics sometimes incorporating feces, other times not; cocoon shape determined by cell shape and without nipple.

ADULT ACTIVITY: Bees predominantly if not completely diurnal, no nocturnal or crepuscular forms reported. Mating not studied, but in some cases known to take place at pollen plants.

CLEPTOPARASITIC BEES: *Exomalopsis* species parasitized by cuckoo bees belonging to the Nomadini (*Hypochrotaenia, Paranomada, Triopasites, Melanomada,* and *Hesperonomada*). Cuckoo bees of other genera not reported, except for unnamed species belonging to the subfamily Nomadinae, tentatively associated with *Tapinotaspis tucumana.*

LITERATURE CITED

Batra, S. W. T.
1972. Some properties of the nest-building secretions of *Nomia, Anthophora, Hylaeus* and other bees. Jour. Kansas Ent. Soc., vol. 45, pp. 208–218.

Bohart, G. E.
1970. The evolution of parasitism among bees. Forty-first Honor Lecture, the Faculty Association, Utah State Univ., pp. 1–33.

Brèthes, Juan
1909. Una anthophorina parasita? Am. Mus. Nac. Buenos Aires, series 3, vol. 12, pp. 81–83.

Claude-Joseph, F.
1926. Recherches biologiques sur les Hymenopteres du Chili (Melliferes). Ann. des Sci. Nat., Zool., series 10, vol. 9, pp. 113–268.

Cane, James H.
1983. Preliminary chemosystematics of the Andrenidae and exocrine lipid evolution of the short-tongued bees (Hymenoptera: Apoidea). Jour. Systematic Zool., vol. 32, pp. 417–430, 2 figs.

Hicks, C. H.
1936. Nesting habits of certain western bees. Canadian Ent., vol. 68(3), pp. 47–52.

Houston, T. F.
1975. Nests, behaviour and larvae of the bee *Stenotritus pubescens* (Smith) and behaviour of some related species (Hymenoptera: Apoidea: Stenotritinae). Jour. Australian Ent. Soc., vol. 14, pp. 145–154.

Hurd, Paul D., Jr., and E. Gorton Linsley
1975. The principal *Larrea* bees of the Southwestern United States (Hymenoptera: Apoidea). Smithsonian Contrib. to Zool., no. 193, pp. 1–74.

Janvier, H.
1955. Le nid et la nidification chez quelques abeilles des Andes tropicales. Ann. des Sci. Nat., Zool., ser. 11, vol. 17, pp. 311–349, 22 figs.

Linsley, E. G.
1945. A new species of *Paranomada* with notes on *Melecta thoracica* Cresson. Ent. News, vol. 56, pp. 149–153.

Linsley, E. G., J. W. MacSwain, and C. D. Michener
1980. Nesting biology and associates of *Melitoma*. Univ. California Pubs. Ent., vol. 90, pp. 1–45, 8 figs.

Linsley, E. G., J. W. MacSwain, and Ray F. Smith
1954. A note on the nesting habits of *Exomalopsis solani* Cockerell. Pan-Pacific Ent., vol. 30, pp. 263–264.

Malyshev, S.
1935. The nesting habits of solitary bees. A comparative study. Eos, Madrid, vol. 11, pp. 201–309.

Michener, Charles D.
1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bull. Amer. Mus. Nat. Hist., vol. 82, pp. 151–326.
1954. Bees of Panamá. *Ibid.*, vol. 104, pp. 1–176, 155 figs., 3 tables.
1966. Evidence of cooperative provisioning of cells in *Exomalopsis* (Hymenoptera: Anthophoridae). Jour. Kansas Ent. Soc., vol. 39(2), pp. 315–317.
1974a. Further notes on nests of *Ancyloscelis* (Hymenoptera: Anthophoridae). *Ibid.*, vol. 47, pp. 19–22.
1974b. The social behavior of the bees. A comparative study. Cambridge, Harvard Univ. Press, pp. 1–404.

Michener, Charles D., and Rudolf B. Lange
1958. Observations on the ethology of neotropical Anthophorine bees (Hymenoptera: Apoidea). Univ. Kansas Sci. Bull., vol. 39, pp. 69–96.

Michener, Charles D., Rudolf B. Lange, Joao J. Bigarella, and Riad Salamuni
1958. Factors influencing the distribution of bees' nests in earth banks. Ecology, vol. 39, pp. 207–217.

Michener, Charles D., and Jesus S. Moure, C.M.F.
1957. A study of the classification of the more primitive non-parasitic anthophorine bees (Hymenoptera, Apoidea). Bull. Amer. Mus. Nat. Hist., vol. 112, pp. 395–452.

Neff, John L.
[In press] Observations of the biology of *Eremapis parvula* Ogloblin, an anthophorid bee with a metasomal scopa (Hymenoptera: Anthophoridae). Pan-Pacific Ent.

Neff, John L., and Beryl B. Simpson
1981. Oil-collecting structures in the Anthophoridae (Hymenoptera): Morphology, function, and use in systematics. Jour. Kansas Ent. Soc., vol. 54, pp. 95–123.

Oliveira, Bernadete Lucas de
1962. Morfologia externa de larva de *Paratetrapedia* (*Paratetrapedia*) *gigantea* (Schrottky, 1909) a considerações filogenéticas sôbre algumas larvas de Anthophoridae (Hymenoptera—Apoidea). Bol. da Univ. do Paraná, Zool., no. 12, pp. 1–21, 3 figs.
1966. Descrição de estádios imaturos de *Lanthanomelissa* sp. (Hymenoptera: Apoidea). Studia Ent., vol. 9, fasc. 1–4, pp. 429–440, 5 figs.

Parker, F. D.
[In press] Biological notes on the bee *Exomalopsis crenulata* Timberlake (Hymenoptera: Anthophoridae). Pan-Pacific Ent., ms. pp. 1–8.

Raw, A.
1976. Seasonal changes in and foraging activities of two Jamaican *Exomalopsis* species (Hymenoptera: Anthophoridae). Biotropica, vol. 8, pp. 270–277.
1977. The biology of two *Exomalopsis* species (Hymenoptera: Anthophoridae) with remarks on sociality in bees. Revista Biologia Tropical, vol. 25, pp. 1–11.

Rozen, Jerome G., Jr.
1977a. The ethology and systematic relationships of fideliine bees, including a description of the mature larva of *Parafidelia* (Hymenoptera, Apoidea). Amer. Mus. Novitates, no. 2637, pp. 1–15.
1977b. Immature stages of and ethological observations on the cleptoparasitic bee tribe Nomadini (Apoidea, Anthophoridae). *Ibid.*, no. 2638, pp. 1–16.
1978. The relationships of the bee subfamily Ctenoplectrinae as revealed by its biology and mature larva (Apoidea: Melittidae). Jour. Kansas Ent. Soc., vol. 51, pp. 637–652.
1984. Nesting biology of diphaglossine bees (Hymenoptera, Colletidae). Amer. Mus. Novitates, no. 2786, pp. 1–33.

Rozen, Jerome G., Jr., and C. Don MacNeill
1957. Biological observations on *Exomalopsis* (*Anthophorula*) *chionura* Cockerell, including a comparison of the biology of *Exomalopsis* with that of other anthophorid groups (Hymenoptera: Apoi-

dea). Ann. Ent. Soc. Amer., vol. 50, pp. 522–529.

Rozen, Jerome G., Jr., Kathleen R. Eickwort, and George C. Eickwort
1978. The bionomics and immature stages of the cleptoparasitic bee genus *Protepeolus* (Anthophoridae, Nomadinae). Amer. Mus. Novitates, no. 2640, pp. 1–24.

Rust, R. W., R. W. Thorp, and P. F. Torchio
1974 The ecology of *Osmia nigrifrons* with a comparison to other *Acanthosmoides*. Jour. Nat. Hist., vol. 8, pp. 29–47, 14 figs.

Schrottky, C.
1901. Biologische Notizen solitärer Bienen von S. Paulo (Brasilien). Allgemeine Zeit. für Ent., Band 6, pp. 209–216.

Stephen, W. P., G. E. Bohart, P. F. Torchio
1969. The biology and external morphology of bees. Oregon State Univ. Press, Corvallis, pp. 1–140.

Timberlake, Philip H.
1980. Review of North American *Exomalopsis* (Hymenoptera, Anthophoridae). Univ. Calif. Publ. Ent., vol. 86, pp. 1–158.

Torchio, Philip F.
1974. Notes on the biology of *Ancyloscelis armata* Smith and comparisons with other anthophorine bees (Hymenoptera: Anthophoridae). Jour. Kansas Ent. Soc., vol. 47, pp. 54–63.

Torchio, Philip F., Jerome G. Rozen, Jr., George E. Bohart, and Marjorie Favreau
1967. Biology of *Dufourea* and of its cleptoparasite, *Neopasites* (Hymenoptera: Apoidea). Jour. New York Ent. Soc., vol. 75, pp. 132–146, 9 figs.

Toro, Haroldo
1976. *Chilimalopsis*, nuevo genero Chileno de Exomalopsini (Hymenoptera: Apoidea). An. del Museo de Hist. Nat. de Valparaiso, vol. 9, pp. 73–76.

Vogel, Stefan
1974. Ölblumen und ölsammelnde Bienen. Tropische und subtropische Pflanzenwelt. Akad. der Wissenschaften und de Literatur, Mainz, pp. 1–267.

Wheeler, W. M.
1919. The parasitic Aculeata, a study in evolution. Proc. Amer. Philos. Soc., vol. 58, pp. 1–40.

Zucchi, Ronaldo
1973. Aspectos bionômicos de *Exomalopsis aureopilosa* e *Bombus atratus* incluindo considerações sobre a evolução do comportamento social (Hymenoptera—Apoidea). Doctoral thesis, Faculdade de Filosophia, Ciências e Letras de Ribeirao Preto, pp. 1–172.